CLASSIFICATION, PHYLOGENY AND ZOOGEOGRAPHIC STUDIES OF SPECIES OF *SATHON* MASON (HYMENOPTERA: BRACONIDAE)

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ABSTRACT

The genus Sathon *is a member of the tribe Microgastrini in the subfamily Microgastrinae of the Braconidae. Ten species are recognized in this study, occurring in the Holarctic and Neotropical regions. Five species have been described:* S. cinctiformis *(Viereck) 1911,* S. eugeni *(Papp) 1972,* S. falcatus *(Nees) 1834,* S. lateralis *(Haliday) 1834 and* S. neomexicanus *(Muesebeck) 1921 (1920). Five species are described as new:* S. aggeris *(type locality Quito-Baeza Rd., Ecuador),* S. circumflexus *(type locality Doolittle Ranch, Colorado),* S. laevidorsum *(type locality Cortez Pass, México),* S. masoni *(type locality Anchorage, Alaska) and* S. papilionae *(type locality Clayoquot, British Columbia). Two species groups are recognized and diagnosed, the* S. lateralis-*group containing* S. lateralis, S. papilionae *and* S. eugeni, *and the* S. falcatus-*group containing* S. laevidorsum, S. aggeris, S. masoni, S. cinctiformis, S circumflexus, S. neomexicanus *and* S. falcatus.

Sathon *is described from characters of adult, larval and cocoon structure, distribution and phylogenetic relationships.* Sathon *is differentiated from other members of the Microgastrini by the possession of a reduced lateral metanotal lobe, in most specimens without setae, with the phragma of the scutellum exposed. New World species of* Sathon *are described and Palaearctic species are diagnosed from the same types of features. Phylogenetic reconstruction shows that the* S. lateralis- *and* S. falcatus-*groups are monophyletic lineages recognized by differences in degree of apotypy and evolutionary trends. The pattern of relationships of* Sathon *species found shows that within the* S. lateralis-*group,* S. papilionae *and* S. eugeni *are sister species, with* S. lateralis *the sister to this sister species pair. In the* S. falcatus-*group, three species pairs are found,* S. laevidorsum + S. aggeris, S. masoni + S. cinctiformis *and* S. neomexicanus + S. falcatus. S. circumflexus *is the sister to* S. neomexicanus + S. falcatus. S. masoni + S. cinctiformis *is closer to the* S. neomexicanus *clade than* S. laevidorsum + S. aggeris. *Phenetic analysis yields a similar set of affinities, with differences only in the placement of* S. circumflexus *and* S. falcatus *as nearest neighbors, and of* S. laevidorsum + S. aggeris *with* S. lateralis-*group species.*

A reconstruction of the geographical history of Sathon *species hypothesizes one vicariance event and three long-distance dispersals combining with several unknown events to result in modern species distributions.*

There are 142 figures and 4 data tables included.

RÉSUMÉ

Le genre Sathon *est membre de la tribu Microgastrini dans la sous-famille Microgastrinae de la famille Braconidae. Dans cette étude, on reconnait dix espèces dans les régions holarctiques et néotropicales. Cinq de ces espèces ont déjá été décrites:* S. cinctiformis *(Viereck) 1911,* S. eugeni *(Papp) 1972,* S. falcatus *(Nees) 1834,* S. lateralis *(Haliday) 1834 et* S. neomexicanus *(Muesebeck) 1921 (1920). Les cinq espéces suivantes sont nouvelles:* S. aggeris *(endroit typique Ch. Quito-Baeza, Equador),* S. circumflexus *(endroit typique Doolittle Ranch, Colorado),* S. laevidorsum *(endroit typique Cortez Pass, Mexique),* S. masoni *(endroit typique Anchorage, Alaska) et* S. papilionae *(endroit typique Clayoquot, Colombie-Brittanique). Deux groupes d'espèces sont reconnus: le groupe* S. lateralis *contenant* S. lateralis, S. papilionae *et* S. eugeni, *et le groupe* S. falcatus *contenant* S. laevidorsum, S. aggeris, S. masoni, S. cinctiformis, S circumflexus, S. neomexicanus *et* S. falcatus.

Le genre Sathon *est décrit à partir des caractères des adultes, larves et pupes, ainsi qu'à partir de sa distribution et de ses relations phylogénétiques.* Sathon *diffère des autres membres de la sous-famille des Microgastrini par la présence d'un lobe métanotal latéral réduit, dans la plupart des spécimènes sans sétas, avec le phragma du scutellum exposé. Les espèces de* Sathon *du Nouveau-Monde sont décrites, et celles du Palaéarctique sont diagnosées à partir des mêmes types de caractères. Une reconstruction phylogénétique démontre que les groupes* S. lateralis- *et* S. falcatus- *sont des lignes monophylétiques reconnues par des différences dans leur degré d'apotypie et de tendances évolutionnaires. Le patron de relations entre les espèces de* Sathon *démontre que dans le groupe* S. lateralis-, S. papilionae *et* S. eugeni *sont des espèces soeurs, et que* S. lateralis *est soeur de cette paire d'espèces soeurs. Dans le groupe* S. falcatus-, *on retrouve trois paires d'espèces:* S. laevidorsum + S. aggeris, S. masoni + S. cinctiformis *et* S. neomexicanus + S. falcatus. S. circumflexus *est soeur à* S. neomexicanus + S. falcatus. S. masoni + S. cinctiformis *est plus rapproché du (((clade)))* S. neomexicanus *que l'est* S. laevidorsum + S. aggeris. *Une analyse phénétique produit des résultats semblables, avec seul des différences dans le placement de* S. circumflexus *et* S. falcatus *comme voisins les plus rapprochés, et* S. laevidorsum + S. aggeris *se retrouvent dans le groupe d'espèces* S. lateralis.

Une reconstruction de l'histoire géographique de Sathon *présente l'hypothèse qu'un évènement de vicariance et trois dispersions à longue-distances combinés avec plusieurs évènements inconnus auraient produits les présentes distributions de* *ces espéces.*

142 figures et 4 tableaux de données sont inclus.

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INTRODUCTION

Sathon Mason is a genus of small (3-6 mm) braconid wasps of the subfamily Microgastrinae. The generic name has not had a long history, being erected by Mason in 1981 and examined in detail for the first time here. Some of the species have been known for many years and have gone through several combinations with various genera as the classification of the Microgastrinae has changed, but have not previously been considered closely related to one another. In the most widely used classification, that of Nixon (1965), two species currently in *Sathon* were placed in the *Apanteles vitripennis*-group (Nixon 1973), three in the *A. falcatus*-group and one was not treated. It was not until Mason's (1981) reclassification that emphasis was placed on host preference and type of female genitalia and a relationship between the species of *Sathon sensu* Mason was proposed. The two species in the *A. vitripennis*-group, *S. lateralis* Haliday and *S. eugeni* Papp (= *A. fausta* Nixon 1973), were unusual in this species group in that females possess long ovipositors and sheaths, unlike the short structures of other species. Mason (1981) recognized the short ovipositor and sheath (= third valvula), along with a suite of other characters, as apotypic. *S. lateralis* and *S. eugeni*, lacking these apotypies, were removed from the *A. vitripennis*-group and placed in a different tribe, the Microgastrini, where they were united with species of the *A. falcatus*-group on the basis of apparent synapotypies in the structure of the metanotum and propodeum.

As constituted in this paper, the genus *Sathon* contains species whose features are unusual in the Microgastrini and convergent with states found in more apotypic tribes, such as the Cotesiini. The synapotypy of *Sathon* species given the most weight by Mason (1981) is a reduced metanotum without setae on the lateral lobe. Also discussed by Mason is reduction of the median carina of the propodeum. *Sathon* is also unusual within the Microgastrini in that some species parasitize macrolepidopterans (*e.g.*, Noctuidae). Although little is known about the life history of *Sathon* species and few have been reared, records indicate that they may be solitary parasitoids of microlepidopterans (Paddock 1933), or gregarious parasitoids of macrolepidopterans (R. Oetting, pers. comm.). All records indicate emergence of parasitoid larvae from a late instar of the host larva, which implies oviposition in an early instar. Oviposition in the host egg is doubtful, at least for gregarious species. Parasitism of macrolepidopterans, nearly universal in apotypic tribes such as the Cotesiini, is unknown in the Microgastrini outside of *Sathon*.

The presence of unusual apotypic features in *Sathon* species makes the genus a candidate for understanding the evolution of the entire subfamily, since major trends in evolution of the subfamily seem to have been in areas of host choice and oviposition structures and behavior (Mason 1981). *Sathon* species display host choice and structural characteristics of both of the two basic types of microgastrines, microlepidopteran-parasitizing and macrolepidopteran-parasitizing. Although no major analysis of host choice evolution in *Sathon* is presented because data are insufficient, it is hoped that this review will provide a framework on which such a study can be based.

A possible secondary consideration in the study of this genus is use in biological control. The economic potential of *Sathon* species is unknown, but some species have been reared from important pest lepidopterans such as the European Pine Shoot moth, *Rhyacionia buoliana* Schiffermüller, the Wax Moth, *Galleria mellonella* (L.) and *Protagrostis obscura* Barnes and McDunnough, a noctuid pest of the bluegrass seed industry. The gregarious larval habit of some *Sathon* species offers potential of rearing the large numbers of parasitoid adults necessary for biological control.

The purpose of this project is to examine the evolution and diversity of the genus *Sathon*. Western hemisphere species are examined in detail, and Palaearctic species are also reviewed. I characterize the species, especially with reference to features useful in determining relationships. I use these characters to explore the evolutionary relationships among species and to reconstruct a phylogeny. From this phylogeny I propose a species-group classification and make brief inferences about evolutionary trends in *Sathon*. Although this study suffers from a paucity of material for some species, I also give a brief discussion of zoogeographic relationships.

MATERIALS AND METHODS

Materials

This study is based on examination of 902 specimens, borrowed from persons or museums listed below. Where possible codons for museums were taken from Heppner and Lamas (1982). Others were designated by me. The codens listed here are also used in species descriptions to indicate deposition of specimens.

AEI	American Entomological Institute, 3005 S.W. 56th Avenue, Gainesville, Florida, USA 32608 (H.K. Townes)
BMNH	Department of Entomology, British Museum (Natural History), Cromwell Road, London, England SW7 5BD (T. Huddleston).
BWC	Bob Wharton Collection, Department of Entomology, Texas A&M University, College Station, Texas, USA 77843.
CAS	California Academy of Sciences, Golden Gate Park, San Francisco, California, USA 94118 (W.J. Pulawski).
CNC	Canadian National Collection, Biosystematics Research Centre, K.W. Neatby Building, Ottawa, Ontario, Canada K1A 0C6 (W.R.M. Mason).
CU	Cornell University Insect Collection, Department of Entomology, Cornell University, Ithaca, New York, USA 14853 (Q.D. Wheeler).
DJMW	Daryl J.M. Williams Collection, Department of Entomology, University of Alberta, Edmonton, Alberta, Canada T6G 2E3.
FSCA	Florida State Collection of Arthropods, Division of Plant Industry, Florida Department of Agriculture, Dolye Connor Building, Gainesville, Florida, USA (J. Wiley).
JWC	James Whitfield Collection, Department of Entomology, 137 Giannini Hall, University of California, Berkeley, California, USA 94720.
LMU	Der Ludwig-Maximilians Universität, Lehrstuhl für angewandte Zoologie, Amalienstrasse 52 Gg D-8000, München 40, Federal German Republic (E. Haeselbarth).
NRS	Naturhistoriska Riksmuseet, Sektionen för entomologi, S-104 05 Stockholm 50, Sweden (K.J. Hedqvist).
OSUC	Department of Entomology, Oregon State University, Corvallis, Oregon, USA 97331 (J.D. Lattin).

RNHL	Rijksmuseum van Natuurlijke Historie, Raamsteeg 2, Postbus 9517, 2300 RA Leiden, Netherlands (C. van Achterberg).
SMEK	Snow Museum of Entomology, Department of Entomology, University of Kansas, Lawrence, Kansas, USA 66045 (D. Wahl).
UCB	University of California, College of Agriculture, Division of Entomology and Parasitology, Berkeley, California, USA (L.E. Caltagirone).
UCD	Department of Entomology, University of California, Davis, California, USA 95616 (R.O. Schuster).
UMSP	Department of Entomology, Fisheries and Wildlife, University of Minnesota, 219 Hodson Hall, 1980 Folwell Avenue, St. Paul, Minnesota, USA 55108 (P.J. Clausen).
USNM	Systematic Entomology Laboratory USDA, c/o U.S. National Museum of Natural History, NHB-168 Washington, D.C., USA 20560 (P.M. Marsh).

Methods

Preparation of Adults.— For observation and illustration of the oral plate and genitalia of the adult, heads and metasomata were cleared in sodium hydroxide. These body parts were easily dissected from pinned or pointed specimens, as both are narrowly joined to the mesosoma. The mesosoma is customarily glued to the pin or point. Both heads and metasomata yielded easily to pressure from an insect pin. Some specimens separated entirely from the pin or point as they were insufficiently glued to it. In these instances the entire specimen was relaxed in distilled water and the desired part removed. The remainder of the specimen was transferred to 95% ethanol, dried and remounted. Parts were cleared using standard techniques and were stored in glycerine on well slides.

Preparation of Larvae.— Exuviae of last instar larvae were obtained by dissection of cocoons. A line of perforations down the longitudinal axis of a cocoon was made with an insect pin and the resulting fissure was pulled open with a pair of forceps. This action fragmented the cocoon and loosened the meconium and exuviae in the bottom. The meconium and exuviae were removed from the bottom of the cocoon with a minuten pin mounted on a handle and moistened to cause the desired material to adhere to it. The meconium and exuviae were cleared in sodium hydroxide and a permanent slide mount in Canada Balsam was made of each exuviae after examination and drawing.

Measurements.— In descriptions, morphometric characters are discussed as ratios with most measurements given as ranges, followed by sample means and standard deviations in brackets (table 6). However, some size comparisons are not amenable to proper measurement because of imprecision, but are still useful in discriminating species. An example of this is ovipositor length, expressed relative to the length of the hind tibia. This character is very useful in separating species, displaying slight intraspecific variation. It is very difficult to measure accurately however, since the base of the ovipositor is hidden by the hypopygium. T9 of the metasoma (see 'Terms'), to which the ovipositor is attached, is tilted anteriorly in some specimens, causing retraction of the visible portion. In females with relatively short ovipositors, the difference in visible length between fully retracted and fully extended states can be half of the actual length.

For characters where relative dimensions are important, but measuring error prevents a quantitative treatment, a qualitative approximation is given. These characters are not included in table 6. If the character is important in phylogenetic reconstruction or is useful in identification, then a figure is also given. Refer to figures 1 to 7 for illustration of measurement methods.

All measurements were made with a Wild M5 stereoscopic dissecting microscope equipped with a numbered measuring bar eyepiece and a doubling lens over the objective. A camera lucida was also installed for drawings and was not removed for measuring. All measurements were transformed into ratios of the dimensions of a structure or the size of one structure relative to another. Ranges, means and standard deviations were then calculated from the ratios. In the description of *Sathon papilionae* new species, ranges only are given. The mean and standard deviation calculated from a sample size of two were not useful. Each specimen was measured for every morphometric character where possible, or another specimen was substituted for any two compared measurements if not. Therefore, the sample size in any species is the same for every measurement and is reported in table 6 with measurements. Sample sizes were chosen to include the maximum range geographically and morphologically. Measurements are intended strictly for descriptive purposes. Statistical analyses were not performed.

Drawings.— Line drawings were made with the aid of a microscope equipped with a camera lucida. Rough sketches were made on drawing paper and later refined and inked onto drawing film. Setae that obscured other features were omitted. Drawings of larval head capsules were made from specimens in well slides with a Leitz Wetzlar SM-LUX transmission microscope. Heads and metasomata of adults, for oral plate and genitalia drawings, were transferred to glycerine jelly (using the formula of Pantin 1969) and arranged in the desired alignment before the jelly set. They were then drawn in the same manner as the larvae. Other drawings were made from pinned or pointed dry adult specimens. Most specimens were drawn with a Wild M5 stereocopic dissecting microscope.

For *Sathon aggeris* new species, some line drawings were taken from prints of Scanning Electron Photomicrographs (see below). Some photomicrographs obtained for this species were too poor in quality to be reproduced, since the specimen was uncoated (see below). Prints were used as templates, and drawings were traced from them and transferred to drawing film. Therefore, some illustrations that appear as photomicrographs in other species treatments are rendered as line drawings for *S. aggeris*. The holotype of *S. aggeris* and the type material of *S. laevidorsum* were not dissected. Therefore, drawings of the female genitalia were taken from point-mounted specimens.

Photomicrographs.— Photomicrographs were taken with a Cambridge 250 Stereoscan Scanning Electron Microscope (S.E.M.). Specimens were removed from their pins or points and their wings were removed and placed on a separate card. Specimens were then cleaned with detergent and ultrasonication and critical point dried. Then they were mounted individually on aluminum stubs with the legs separate. Specimens of species except those of *Sathon aggeris* were coated with gold and examined with the S. E. M. The *S. aggeris* female was not so coated because it is the holotype and only known female.

Terms.— Terms for features of the larval head capsule are taken from Capek (1970). Terms for features of adult structures taken from Townes (1969), except terms for: male external genitalia taken from Snodgrass (1941); female genitalia from Ross (1945) and wing venation, taken from Mason (1981)[1].

Some terms and abbreviations not found in the above references are defined below. Codens for the terms are given before the definitions (see also fig. 1).

POL	Posterior ocellar line is the shortest distance between the lateral (= posterior) ocelli.
LOL	Lateral ocellar line is the shortest distance between a lateral ocellus and the anterior ocellus.
OOL	Ocular Ocellar line is the shortest distance between a lateral ocellus and a compound eye margin.
AOD	Anterior ocellar diameter is the greatest diameter of the anterior ocellus.
LOD	Lateral ocellar diameter is the greatest diameter of a lateral ocellus.
T1 to T9	Metasomal Terga 1 to 9 (= abdominal terga 2 to 10).
Island	A small oval area of subtle sculpture on terga 3 to 7 of the metasoma, dorsad the spiracle. The sculpture is subdued in most specimens to the point that the spot is only visible by the difference in light reflection from the surrounding tergum. This term was coined by Mason (1978), but has not been widely used.
Oral plate	A sclerite on the anterior surface of the pharynx. It is anteriorly concave, and has one pair each of dorsal and ventral arms. The ventral arms connect to either side of the epipharynx. A pair of lateral rows of oval 'windows' of thin cuticle parallel the sides of the plate. This term was coined by Williams (1985) (fig. 17).

Descriptive Format.— One basic sentence structure is used in all descriptions. Each sentence treats a single structure. If a structure includes more than one character useful for descrimination of species, these characters are separated by semicolons. In this way the name of the structure is repeated as seldom as possible

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[1] Mason (1981) uses the terms for wing venation proposed by Eady (1974), but has numbered the abscissae of each vein. There is a departure from the Eady system in Mason's treatment of the radial sector (Rs) vein. This paper does not follow that departure (see fig. 7 this paper versus fig. 1, Mason 1981).

and there is little confusion about which structure a character is part of. Exceptions occur when the description of a character is so long, or when there are so many characters in a structure, that confusion results if the name of the structure is not repeated. Figure numbers are given in one of two places for each sentence with an accompanying figure. If the sentence includes more than one character the figure number of the structure is given immediately after the name of the structure. All character states are found on that figure. If the sentence includes only one character, the figure number is given at the end of the sentence.

The generic description serves two purposes. It characterizes *Sathon* relative to other genera in the subfamily, and displays the range of variability of characters within the genus. These functions are not discriminated in the description except in the diagnosis, which contains only characters for discrimination of *Sathon*. The list of references about *Sathon* species in the synonymy section of the generic description is not a complete listing. Most references refer to Palaearctic species which are not examined in detail in this study, originally described in other, currently valid genera. Therefore, records of Palaearctic species are limited to significant taxonomic references. The reader is referred to Shenefelt (1972) for regional lists, life history references, etc. This format is also followed in diagnoses of Palaearctic species.

Characters that are consistent within *Sathon* are not repeated in species descriptions. Species descriptions characterize species relative to other *Sathon* species only. New World species are fully described, but Palaearctic species have been treated four times since 1945 (Wilkinson 1945, Nixon 1965 and 1973, Papp 1983), and so are only diagnosed. These diagnoses are designed primarily for identification, and are not of the same format as full descriptions, with one exception. Characters of the female genitalia have not been treated adequately by previous authors. Given the importance of female genital characters in *Sathon* phylogeny, these characters are fully described in each diagnosis. Some characters found in Palaearctic species that do not appear in the diagnoses are noted in sections 'Reconstructed Phylogeny' and 'Phenetic Analysis', and Appendix 1 (table of ratios).

Three formats are used for locality data in the descriptive section. New species have all localities listed as type material, with distributions summarized from localities listed. Previously described New World species have sections for type material examined and distribution, with lists of localities personally examined given in appendix 2. Distribution data are summarized from the information in the appendix. Range maps are given for New World species. Type material was not available for Palaearctic species, although specimens determined by designators of neotypes and the author of the holotype were examined. Therefore, in each description there are separate sections for neotype or holotype and distribution, with ranges summarized from published records. Material personally examined for the three Palaearctic species is listed in appendix 2 along with material examined for previously described Nearctic species. Range maps are not provided for Palaearctic species.

Labels on holotypes of new species are reported with slashes separating contents of different lines or labels. Other labels have not been so treated. The contents of these labels have been reported exactly as originally printed. Locality data have been altered in two ways. For some series of specimens from the same locality, data for different dates or collectors are summarized and the locality is given once only. This method of summarization is used only where the information is clear. For popular localities collected by numerous individuals at numerous times (*S. neomexicanus* Muesebeck taken from Sagehen, California for example. Appendix 2), the labels are not summarized. On some labels, data given are insufficient for convenient identification of localities. For such labels, additional information which does not appear on the labels is included in square brackets.

In descriptions and various discussions, characters states are referred to as belonging to certain species or species groups. It is here acknowledged that these states actually belong to *individuals* of these taxa, but are ascribed to the entire taxon to avoid numerous repetitions of the words 'specimens of', 'adults of', 'larvae of', *etc.*

Criteria for Species Discrimination.— The application of biological (Mayr 1963) or evolutionary (Simpson 1951, Wiley 1978) species concepts to a systematic study of a collection of preserved material presents great practical difficulty. The major portion of such concepts include such dynamic phenomena as reproductive isolation and evolutionary change through time, neither of which are represented conclusively in preserved specimens. Therefore, the emphasis in this study has been placed on two criteria, phenetic and distributional characters, that give evidence of species status of populations. Two populations that retain phenetic distinctiveness in spite of overlap of geographic range are considered to be reproductively isolated from one another and are therefore assumed to be separate species. The degree of phenetic difference between such species is used as an estimate of species status in phenetically distinct populations that are geographically isolated.

Criteria for Discrimination of Species Groups.— Species groups are monophyletic units defined by several shared derived character states. Each group shows unique differences in relative importance of character systems in evolution. The *S. falcatus*-group displays marked trends in the evolution of genitalia in both sexes (see 'Evolutionary Trends') whereas the *S. lateralis*-group does not. Species of the *S. lateralis*-group are relatively similar to one another in habitus, displaying slight character evolution, whereas species of the *S. falcatus*-group are relatively more divergent from one another.

TAXONOMIC TREATMENT OF THE GENUS

The genus *Sathon* was erected by Mason (1981) for Nixon's (1965) *falcatus*-group of *Apanteles* Förster, part of Nixon's *A. vitripennis*-group and a North American species Nixon did not treat. When Mason (1981:78) erected *Sathon*, he expressed some doubt about the placement of the species taken from the *A. vitripennis*-group [*S. lateralis* Haliday and *S. eugeni* Papp (=*S. fausta* Nixon)], because of the absence of some derived character states shared by other species of *Sathon*. *S. lateralis* and *S. eugeni* share the retracted and glabrous lobe of the metanotum and the reduced median carina of the propodeum with other *Sathon* species, but lack the truncate paramere of the male and the variously developed, specialized shape of the posterodorsal margin of the female hypopygium.

Examination of several species of *Choeras* Ashmead, the genus most closely related to *Sathon*, has revealed that the synapotypies between the species taken from the *A. vitripennis*-group and other *Sathon* species are not very reliable. Some specimens of *Choeras* exhibit a partially retracted (although setose) metanotal lobe and a partially reduced median propodeal carina. Also, some specimens of *Sathon* exhibit a few setae on the metanotal lobe and others display an almost complete propodeal carina. However, *Choeras* is a large and inadequately understood genus. Without substantial revisionary work and analysis of character evolution and distribution in the genus, I cannot make a conclusion about the reliability of the metanotal and propodeal characters that define *Sathon*. I therefore retain *S. lateralis* and *S. eugeni* in *Sathon*.

Sathon is organized in two species groups– the *S. lateralis*-group which contains the two species above plus *S. papilionae*, and the *S. falcatus*-group which contains the rest of the species in the genus. The *S. lateralis*-group is considered less apotypic than the *S. falcatus*-group because of the characters dicussed above (see also 'Evolutionary Trends'), with one exception. All species in the *S. lateralis*-group have the median carina reduced to a trace or lost completely, whereas species of the *S. falcatus*-group have retained a trace or have the median carina partially developed. The name for the *S. falcatus*-group has been retained from Nixon (1965), despite the inclusion of the type species of *Sathon*, *S. neomexicanus* Muesebeck. Nixon's *A. falcatus*-group contains the same previously described species as my *S. falcatus*-group. His *A. falcatus*-group is characterized by the truncate male paramere, agreeing with my characterization.

Dissection of female genitalia revealed that some species that had been placed by Mason in *Sathon* do not belong in the genus. Dissections of females of *Lathrapanteles papaipemae* Muesebeck and three previously undescribed species revealed genitalia similar to those of the Cotesiini, whose species parasitize macrolepidopterans and are more apotypic than species of the Microgastrini. These microgastrine taxa were described as members of the genus *Lathrapanteles*, which was erected to accommodate them.

Lathrapanteles papaipemae females have a robust T9 of the metasoma, anterior apodeme of T9, and second valvifer. Moreover,the third valvula is attached near the base of the second valvifer. Examination of the last instar larval integument of *L. papaipemae* showed features common to cotesiine larvae. In all, *L. papaipemae* and the three previously undescribed species are apotypic in 10 of 14 characters used by Mason (1981, Table 2) to characterize the macrolepidopteran-parasitizing Microgastrinae, whereas *Sathon* species are apotypic in only three (or in apotypic *Sathon* species, five. Williams 1985).

Sathon Mason

Sathon Mason 1981.

Microgaster, Haliday 1834: 242, 248 (in part). --Nees von Esenbeck 1834: 175 (in part). --Curtis 1837: 116, 117 (in part).

Apanteles; Marshall 1872: 104, 105 (in part). --Muesebeck 1921 (1920): 526, 529 (in part). --Muesebeck 1922: 16 (in part). --Gautier & Cleu 1927: 85 (in part). --Wilkinson 1937: 463 (in part). --Fahringer 1938: 9 (in part). --Hincks 1944: 20 (in part). --Wilkinson 1945: 121, 133 (in part). --Strickland 1946: 37 (in part). --Muesebeck and Walkley 1951: 125, 131 (in part). --Muesebeck 1958: 29 (in part). --Nixon 1965: 186 (in part). --Muesebeck 1967: 41, 43 (in part). --Shenefelt 1972: 551 (in part). --Papp 1972: 336 (in part). --Nixon 1973: 177, 186 (in part). --Papp 1983: 260 (in part).

Sathon Mason 1981: 78 (description). Type species *Apanteles neomexicanus* Muesebeck 1921 (1920). Original designation. --Williams 1985: 1962 (some species removed from *Sathon*).

Diagnosis.— Adults of *Sathon* are differentiated from those of other genera of Microgastrinae by the following combination of character states: metanotum with sublateral lobes slight asetose convexities (some specimens of *S. eugeni* with few setae); propodeum with median carina present over most of length or almost completely absent, but marked by at least a trace of rugosity; T1 of metasoma somewhat narrow, length approximately three times apical width or more; T2 subtriangular; hypopygium evenly sclerotized and without striae midventrally; ovipositor and third valvula at least 0.5 times as long as hind tibia; third valvula partly to completely polished and shining, attached near apex of second valvifer; T9 height 2.0 or more times width; second valvifer slender, narrow at apex.

Description.— **Female**. *Color.* Head and mesosoma rufopiceous to black; metasoma black, with white or fulvous spot on anteriormost laterotergites, to almost completely fulvous except for rufopiceous terga at base and apex of metasoma; antenna brown or black, some species with scape fulvous; legs fulvous or rufofulvous, some species with piceous coxae or areas on femora or tibiae and tarsi; third valvula fulvous to piceous.

Head. Width 1.54 - 2.08 times length. Occiput narrowly and shallowly (fig. 1) or broadly and somewhat deeply (fig. 134) indented medially, but not distinct from vertex and genae. Clypeus 2.50 - 3.90 (fig. 2) times wide as high; dorsal margin obscure or distinct and ventral margin with or without reflexed rim. Face with median carina on dorsal 0.2 to 0.4. Malar space sculptured or smooth posteriorly, furrow from ventral margin of eye to anterior mandibular articulation present or absent. POL/OOL = 0.62 - 1.78; POL/LOL = 1.75 - 3.25; LOD/AOD = 0.89 - 1.43; LOL/AOD = 0.47 - 1.33 (fig. 1). Penultimate flagellomere width 0.50 - 1.00 times length (fig. 5). Oral plate markedly narrowed ventrally or not, with or without median lines or area of pigmentation, dorsal margin concave to convex (figs. 17, 32, 35, 77, 90, 103, 117, 131).

Mesosoma. Pronotum (figs. 8, 23, 38, 45, 61, 68, 81, 94, 108, 122) with dorsal groove straight or decurved and smooth to moderately sculptured; ventral groove faintly sculptured to markedly foveolate and rugose anteriorly; ventral margin sinuate; ventral polished band width at posteroventral angle three to more than five times width at collar, smooth or striate posteriorly, band bottle shaped or not, with sinuation of ventral margin and ventral groove matched or not; pronotal disc with slight to distinct punctures on dorsal 0.33 or more of surface; discal pit slight to distinct. Propleuron striate or punctate posterolaterally.

Mesoscutum with punctures obscure to moderately developed on posterior part; setae posteriorly directed on anterior half, but posteromedially directed on posterior half in some species, line of setal convergence present or absent. Prescutellar furrow (figs. 9, 24, 39, 46, 62, 69, 82, 95, 109, 123) straight or arcuate, with anterior margin obscure or distinct; foveolae faint, especially medially, or distinct throughout. Scutellum (figs. 10, 25, 40, 47, 63, 70, 83, 96, 110, 124) with lunule as wide as or narrower than costate area, with dorsal margin evenly convex or irregular; costate area with costae absent medially or present throughout, in some species irregular carinae extended between costae; dorsal margin of costate area smooth or with sculpture on median polished part of scutellum; posterior margin of scutellum with slight or distinct median lobe. Metanotum (figs. 12, 27, 42, 49, 55, 72, 85, 98, 112, 126) with lateral convexity or moderate sublateral lobe, lobe without setae (except in some specimens of *S. eugeni* Papp); posterior margin simple or with foveolate rim; medial pit slightly sculptured or smooth, with sides straight, irregular or anteriorly divergent; lateral pits nearly smooth to markedly sculptured, narrower or wider than part of metanotum anterior to pit, with or without a well delimited anterior margin. Metapleuron (figs. 11, 26, 41, 48, 71, 84, 97, 111, 125) with median groove obsolete or distinct and sculptured; sculpture on posterior portion of metapleuron slight and limited to extreme posterior end or marked and covering most of surface; posteroventral carina angulate and widened or round and narrow near hind coxa. Propodeum (figs. 12, 27, 42, 49, 55, 72, 85, 98, 112, 126) smooth and with distinct punctures to areolate rugose, with or without lateroapical tubercles; median carina extended over most of propodeal length but absent at extreme base, or absent except as trace of rugosity; spiracle round to elongate oval, separated from pleural carina by 0.5 or more of its least diameter, in some species connected to pleural carina by carina or raised area; medioapical boss round, medially thickened, or triangular.

Tarsal claws longer or shorter than width of apical tarsomere. Penultimate fore tarsomere length 1.00 - 1.83 times width. Inner midtibial spur slightly to nearly twice as long as outer and 0.75 to as long as middle basitarsus. Inner hindtibial spur subequal to or slightly longer than outer, less or slightly more than 0.5 as long as hind basitarsus. Head width 0.88 - 1.53 hind coxa length; punctures on hind coxa absent, present in longitudial band or distinct on lateral surface (figs. 14, 29, 44, 52, 58, 74, 87, 100, 114, 128).

Fore wing (fig. 6) with stigma approximately 2.0 - 3.0 times long as wide; 1Rs shorter or longer than thickness of SC+R and inserted basally or subbasally on parastigma; 2A present or absent; 2r length 0.57 - 1.83 2Rs length; 1Rs+M curved, nearly straight, or sinuate; 1Rs+M length 0.92 - 1.26 1M length; 1Cu1 length 0.74 - 1.39 m-cu length. Hind wing with Cu+cu-a evenly curved or sinuate; SC+R with bulb at extreme base that protrudes above upper plane of wing (figs. 54, 67), or only with slight convexity.

Metasoma. T1 (figs. 13, 28, 43, 50, 56, 73, 86, 99, 113, 127) narrow, at least 3.0 times longer than wide at apex; smooth over most of surface to markedly rugose; apex narrower than base, with straight, curved, or slightly sinuate sides; apex slightly to extremely convex medially. T2 (figs. as for T1) subtriangular, with lateral margins straight, curved, slightly sinuate, or obscured by rugosity; rugose, some species with median smooth area; apical margin straight, curved, or sinuate. T3 smooth or sculptured at extreme base; setae evenly distributed except for small or moderately large mediobasal area; apex desclerotized and whitened or not. T4 to T7 desclerotized and whitened or not; setae limited to single apical row medially, or evenly distributed. Island oval to elongate oval, in one species keyhole-shaped, progressively more elongate toward metasoma apex. Hypopygium (figs. 18, 33, 36, 53, 64, 78, 91, 104, 118, 132) with setae absent midventrally along length or only at midlength; apex entire or emarginate; median ventral area evenly sclerotized and without striae; posterodorsal margin straight, angulate, or sinuate, with or without subapical lobe. T9 (figs. 16, 31, 34, 76, 89, 102, 116, 130) approximately 2.0 to 3.0 times high as wide; anterior apodeme slightly developed. Second valvifer (figs. as for T9) slender, narrowed apically; short and not extended into dorsal 0.5 of T9, or long and extended nearly to dorsal margin of T9; apex rounded, irregular, immarginate, or with differentiated head or apodeme. Third valvula (figs 16, 31, 34, 53, 64, 76, 89, 102, 116, 130) 0.47 - 1.28 times length of hind tibia; partly to completely polished; attached to second valvifer near valvifer's apex; straight or decurved, ventral margin convex or concave and extensively desclerotized or evenly sclerotized; setae on apical 0.66 or more, evenly distributed or concentrated on ventral half, in one species apical setae bent-tipped; apex with narrow and triangular or broad desclerotized area. Ovipositor decurved, evenly (figs. 16, 31, 34, 53, 64, 89, 102) or markedly more near apex than near base (figs. 76, 116, 130); approximately 1.0 to 2.0 times as long as hind tibia, with or without subapical constriction; basal bulb slightly (figs. 16, 31, 35) to markedly (figs. 76, 89, 102, 116, 130) set off from shaft.

Male. Similar to female, except: in most species color tones of most body parts darker than in female; antenna elongate relative to female, penultimate flagellomere width at most 0.5 times length; propodeum with sculpture less developed than female in most species (figs. 15, 59, 75, 88, 101, 115, 129); T1 and T2 of metasoma (figs. as for propodeum except *S. aggeris* where it is fig. 60) slender relative to female, in some species with less developed sculpture; paramere rounded or truncate and narrowed or markedly widened at apex (figs. 21, 22, 65, 66, 79, 80, 92, 93, 106, 107, 120, 121, 135, 136), sides curved or nearly straight; aedeagus ovoid or triangular in cross section and slightly or distinctly knobbed at apex; digitus short or elongate (figs. as for paramere); basal ring medially sclerotized or desclerotized, with or without median carinae (figs. as for paramere).

Cocoon. White, solitary or in oblong mass.

Larva (figs. 19, 37, 119, 133). Solitary or gregarious. Hypostoma with one to three mandibular processes and small or marked spur; mandible blade straight or curved and with row of straight and regular or irregular teeth on apical 0.50 to 0.66; silk press with thin or thick integument, internal details not or extensively visible in cleared specimens; labial sclerite wider than high or higher than wide.

Hosts.— Hosts are known only for *S. lateralis*, *S. papilionae*, *S. eugeni*, *S. falcatus* and *S. neomexicanus*. These species have been reared from lepidopterous larvae of the following families: Geometridae, Glyphipterygidae, Gracillariidae, Hepialidae, Lymantriidae, Noctuidae, Olethreutidae, Papilionidae, Pterophoridae, Pyralidae, Sesiidae and Yponomeutidae.

Distribution.— The range of this genus extends throughout the Holarctic region, and also into the Neotropical (as far south as Colombia) and Oriental (Java) regions.

Chorological and Phylogenetic Affinities.— *Sathon* species are sympatric with *Choeras* Ashmead species, as the latter genus is cosmopolitan. The significance of this is unknown as the exact relationship between the genera is uncertain.

Sathon is apparently closely related to *Choeras*, from which it differs only in the structure of the metanotum and hypopygium. I have examined several undescribed species of *Choeras* that are very similar to *S. lateralis*-group species. One such species is included in the outgroup used for character polarization (see 'Reconstructed Phylogeny'). It is not currently known if the diverse genus *Choeras* is delimited by any synapotypies relative to *Sathon* or any of the more derived genera in the tribe. Given the similarity of some apotypic *Choeras* species to *Sathon*, it is possible that *Choeras* is paraphyletic to *Sathon*. It is also possible that the *S. falcatus*- and *lateralis*-groups are independently derived from *Choeras* stock. This possibility is suggested by the retention of submedial metanotal setae in some specimens of *S. eugeni* Papp, which reduces the value of the primary diagnostic feature of *Sathon* species relative to other members of the tribe. Unfortunately, the majority of *Choeras* species are unknown, and the genus is very large. Description of many of the more apotypic species and careful examination of character evolution in this genus must be made before any definite change in the taxonomic status of *Sathon* can occur.

Keys to species of *Sathon* (Females)

1 T2 of metasoma with lateral margins delimited by anteriorly curved grooves (figs. 13, 28, 43). Hypopygium with evenly curved posterodorsal margin (fig. 18). ...... (*S. lateralis*-group) 2

1' T2 of metasoma with lateral margins obscured by rugosity (fig.

73) or delimited by nearly straight grooves (fig. 127). Hypopygium with angulate (fig. 78) or sinuate (fig. 132) posterodorsal margin (weakly sinuate in *S. laevidorsum* new species). .... (*S. falcatus*-group) 4

2 (1) Hind coxa mostly fulvous and with punctures obscure (fig. 44). Palaearctic. .... *S. eugeni* (Papp), p. 548

2' Hind coxa mostly piceous and with punctures distinct (fig. 14). 3

3 (2) Propodeum nearly smooth apically (fig. 27). Hind leg darkened apically but without distinct piceous areas. Nearctic (Alaska). .... *S. papilionae* new species, p. 547

3' Propodeum sculptured apically (fig. 12). Hind leg with distinct piceous area on apex of tibia and usually on apex of femur. Palaearctic. .... *S. lateralis* (Haliday), p. 546

4 (1) Posterior margin of metanotum with rim conspicuous in dorsal aspect (figs. 49, 55). Inner midtibial spur nearly as long as middle basitarsus. 5

4' Posterior margin of metanotum with rim absent or inconspicuous in dorsal aspect (fig. 72). Inner midtibial spur at most 0.75 of middle basitarsus length. 6

5 (4) Propodeum and T1 of metasoma markedly rugose (figs. 55, 56). T1 medially protuberant (fig. 57). Metasoma with white lateral band. Neotropical (Ecuador). .... *S. aggeris* new species, p. 551

5' Propodeum and T1 of metasoma nearly smooth except for a few punctures (figs. 49, 50). T1 slightly convex (fig. 51). Metasoma mostly piceous with anterolateral fulvous area. Nearctic (Mexico). .... *S. laevidorsum* new species, p. 550

6 (4) Propodeum with raised lateroapical carinae and rugosity (fig. 72). Hypopygium with posterodorsal margin angulate (fig. 78). 7

6' Propodeum nearly smooth or with low wrinkles (fig. 126) Hypopygium with posterodorsal margin sinuate (fig. 132). 8

7 (6) Color predominantly piceous except for legs and anteriormost laterotergites of metasoma. Third valvula piceous and with all setae straight (fig. 76). Ovipositor evenly decurved and with marked subapical constriction (fig. 76). Nearctic. .... *S. masoni* new species, p. 553

7' Color predominantly rufopiceous with extensively fulvous metasoma. Third valvula fulvous and with apical setae bent-tipped (fig. 89). Ovipositor sharply decurved at apical 0.33 and without subapical constriction or with very slight one (fig. 89). Nearctic. .... *S. cinctiformis* (Viereck), p. 555

8 (6) Ovipositor (including part hidden by hypopygium) slightly

longer than hind tibia, evenly but markedly decurved over most of length (fig. 102). Nearctic. .... *S. circumflexus* new species, p. 557

8' Ovipositor (including part hidden by hypopygium) approximately twice as long as hind tibia, more decurved apically than basally (fig. 130). 9

9 (8) Occiput narrowly and shallowly indented medially (fig. 1). 3Rs of fore wing slightly sinuate, decurved near wing apex. T1 of metasoma with wide medioapical smooth area (fig. 113). Hypopygium sclerotized and entire apically (fig. 118). Nearctic. .... *S. neomexicanus* (Muesebeck), p. 558

9' Occiput concave medially, head arc-shaped (fig. 134). 3Rs of fore wing straight, usually not decurved near wing apex. T1 of metasoma with narrow or no medioapical smooth area (fig. 127). Hypopygium slightly desclerotized and emarginate apically (fig. 132). Palaeartic. .... *S. falcatus* (Nees von Esenbeck), p. 561

Known Males

1 T1 of metasoma evenly narrowed apically, with sides straight, length approximately 4 times apical width and sculpture absent except in lateroapical areas (fig. 15). T2 with lateral margins delimited by anteriorly curved grooves. Aedeagus ovoid in cross section at midlength. Paramere rounded at apex (fig. 22, *S. lateralis*-group). Palaeartcic. ......*S. lateralis* (Haliday), p. 546

1' T1 of metasoma parallel sided or more gradually narrowed basally than apically, with sides sinuate or curved, length less than 4 times apical width (approximately 4 in *S. circumflexus* n. sp.), and scuplture present over most of surface (figs. 60, 75, 88, 101, 115, 129). T2 with lateral margins obscured by rugosity or delimited by nearly straight grooves. Aedeagus triangular in cross section at midlength. Paramere truncate at apex (figs. 66, 136, *S. falcatus*-group). 2

2 (1) Propodeum with raised carinae and rugosity lateroapically (fig. 75). T2 of metasoma with lateral margins obscured by rugosity (fig. 75). 3

2' Propodeum smooth or with low rugosity lateroapically (fig. 101). T2 of metasoma with lateral margins delimited by grooves (fig. 101).. 4

3 (2) Head and mesosoma rufopiceous, metasoma predominantly fulvous. Hind coxa fulvous. Posterior part of metapleuron extensively punctate and sculptured, with carina extended from

posterior rim (fig. 71). Nearctic. ....*S. cinctiformis* (Viereck), p. 555

3' Body predominantly piceous. Hind coxa piceous basally. Posterior part of metapleuron with few punctures, sculpture limited to area near posterior rim, and without carina (fig. 84). Nearctic.......................................*S. masoni* new species, p. 553

4 (2) Posterior margin of metanotum with foveolate rim (fig. 59). T2 of metasoma with lateral margins delimited by concave grooves (fig. 60). Legs with longitudinal bands of piceous coloration. Neotropical (Ecuador). ....*S. aggeris* new species, p. 551

4' Posterior margin of metanotum without rim (fig. 101). T2 of metasoma with lateral margins delimited by approximately straight grooves (fig. 101). Legs fulvous, darkened apically. 5

5 (4) T1 of metasoma slender, approximately as wide at apex as medioapical boss of propodeum (fig. 101). T2 longer than wide, with posterior margin slightly sinuate (fig. 101). Paramere slightly longer than T1. Nearctic. ....*S. circumflexus* new species, p. 557

5' T1 of metasoma wider at apex than medioapical boss of propodeum (fig. 129). T2 wider than long and with posterior margin markedly sinuate (fig. 129). Paramere longer than T1+T2. 6

6 (5) Fore and middle coxae mostly piceous. Hind coxa entirely piceous, with distinct punctures on most of lateral surface (fig. 128). Parameres in contact midventrally in a broad band at base, apical truncation slightly oblique (figs. 135, 136). Palaearctic....................*S. falcatus* (Nees von Esenbeck), p. 561

6' Fore and middle coxae mostly or entirely fulvous. Hind coxa fulvous at least at extreme apex, with punctures obscure over most of lateral surface except for a midlateral band (fig. 114). Parameres in contact midventrally in a narrow band at base, apical truncation markedly oblique (figs. 120, 121). Nearctic. ... .*S. neomexicanus* (Muesebeck), p. 558

The *S. lateralis*-group

Adults of the *S. lateralis*-group are differentiated from those of the *S. falcatus*-group by the following combination of character states: costate area of scutellum with costae faint or absent over wide medial area (fig. 10); propodeum with median carina short or absent (fig. 12); T2 of metasoma with lateral margins delimited by anteriorly curved grooves and posterior margin nearly straight (fig. 13); T3 with setae evenly distributed except for small mediobasal area; apical unsclerotized and unpigmented area of T6 and T7 more pronounced medially than laterally, both terga somewhat emarginate in specimens with fully expanded metasomata (fig. 20); female with posterodorsal margin of hypopygium evenly curved and with third valvula straight (figs 16, 18); male (where known) with paramere rounded apically and aedeagus ovoid in cross section (fig. 22).

Sathon lateralis (Haliday) 1834
(Figs. 8 - 22)

Microgaster lateralis Haliday 1834: 248; type lost, Neotype designated by Wilkinson 1945: 121.
Apanteles lateralis; Marshall 1872: 105.
Sathon lateralis; Mason 1981: 80.

Neotype.— Male, Bignell Collection, Plymouth Museum. Reg. No. 2076. Designated by Wilkinson (1945: 123).

Diagnosis.— **Female**. *Color*. Head and mesosoma piceous; metasoma piceous, with anterolateral fulvous area on anteriormost laterotergites; antenna piceous; fore and middle legs fulvous, hind leg fulvous with coxa, dorsodistal area of femur, distal end of tibia and all tarsomeres infuscate; third valvula dark rufopiceous.

Head. Oral plate evenly pigmented, with dorsal margin flat but medially desclerotized (fig. 17).

Mesosoma. Pronotum (fig. 8) with dorsal groove smooth or slightly sculptured; ventral groove with slight foveolae. Mesoscutum with punctures obscure on most of surface. Scutellum (fig. 10) with costae moderately distinct, or faint medially and absent anteriorly; anterior groove deep, crossed by very faint to distinct costae; dorsal groove shallow and very narrow anteriorly; posterior margin of scutellum with marked median lobe. Metanotum with moderate convexity or marked sublateral lobe on anterior margin (fig. 12). Propodeum punctate basally, rugose near medioapical boss and in some specimens lateroapically (fig. 12).

Inner midtibial spur longer than outer and nearly as long as middle basitarsus. Hind coxa with punctures distinct (fig. 14).

Metasoma. T1 (fig. 13) smooth mediobasally, rugosopunctate elsewhere; apex narrower than base, with sides straight or slightly sinuate near apex. T2 (fig. 13) with lateral margins slightly to moderately sinuate; rugose, but with sculpture faint or absent medially in some specimens: apical margin slightly convex or slightly sinuate. Hypopygium (fig. 18) with setae absent midventrally; apex entire. T9 approximately 2.0 times higher than wide (fig. 16). Second valvifer projected into upper 0.5 of T9, apex immarginate (fig. 16). Third valvula (fig. 16) with setae evenly distributed; apex with broad desclerotized area. Ovipositor (fig. 16) evenly slightly decurved; approximately as long as hind tibia, without subapical constriction; basal bulb not markedly set off from shaft.

Male. Similar to female, except: some specimens with antenna rufopiceous; medioapical boss triangular in some specimens; T2 with sculpture effaced or lateral margins obscured by rugosity (fig. 15); paramere irregularly rounded and narrowed at apex, length much less than 0.33 of metasoma (fig. 22); aedeagus triangular in cross section at midlength, oval elsewhere, apex slightly knobbed (fig. 22); digitus short, apex scarcely longer than broad (fig. 22); basal ring slightly sclerotized midapically, without median carinae (fig. 21).

Cocoon. Elongate oval, round in cross section, without flattened or slightly translucent sides.

Larva (fig. 19). Gregarious. Hypostoma with one small mandibular process and slight hypostomal spur; mandible blade curved at apex, with single row of straight, regular teeth on apical 0.5; silk press apparently with thin integument, only external details visible; labial sclerite approximately wide as high.

Hosts.— *S. lateralis* has been reared from larvae of the following species of Lepidoptera: *Tephroclystia assimilata* Dbld., *Liparis auriflua* L., *Porthesia chrysorrhoea* L., *Anthophila fabriciana* L., *Yponomeuta padella* L., *Elachista taeniatella* Staint, *Galleria mellonella* L., *Priobium carpini* Hbst. and *Gracillaria syringella* F. (see Shenefelt 1972 for citations of rearing records).

Phylogenetic Affinities.— *S. lateralis* is the sister species to *S. eugeni* + *S. papilionae*.

Distribution.— Western part of the Palaearctic Region. Published records are from Finland to Hungary, and from England to western U.S.S.R.

Chorological Affinities.— The range of this species overlaps with both *S. falcatus* and *S. eugeni*. Specimens of this species have been collected at localities where those of both other species have been found. Apparently sympatric with *S. eugeni*, a member of the sister group of *S. lateralis*.

Sathon papilionae new species
(Figs. 23 - 33)

Holotype.— Female, Papilio zelicaon / Clayoquot / B.C. / No. 61-1491-0A2 / Date 20-VIII-61 / F.I.S. 1961 (CNC).

Derivation of Specific Epithet.— Latin, masculine, referring to the host from which this species was reared.

Diagnosis.— Adults of this species are differentiated from those of other *Sathon* species by the following combination of character states: propodeum smooth or with few wrinkles apically; hind coxa piceous on basal 0.75 and with marked punctation; T1 of metasoma evenly narrowed apically and with sculpture limited to lateroapical areas; T2 of metasoma with lateral margins delimited by sinuate grooves; hypopygium with posterodorsal margin evenly and gradually convex.

Description.— **Female.** *Color.* Head and mesosoma piceous; metasoma with T1 and T2 piceous, apex and venter rufopiceous and laterotergites fulvous; antenna brown; fore and middle legs fulvous, hind leg fulvous with coxa piceous on basal 0.75 and hind tibia rufopiceous at apex; third valvula piceous.

Head. Occiput narrowly and shallowly indented medially. Clypeus with dorsal margin distinct, ventral margin with reflexed rim medially obscure. Face with median carina on dorsal 0.4. Malar space sculptured posteriorly except near eye; furrow from ventral margin of eye to anterior mandibular articulation complete. Oral plate evenly pigmented, with dorsal margin concave (fig. 32).

Mesosoma. Pronotum (fig. 23) with dorsal groove straight and deeply impressed, but smooth; ventral groove slightly foveolate, more foveolate anteriorly than posteriorly, area of junction with dorsal groove smooth; ventral margin slightly sinuate; width of ventral polished band at posteroventral angle approximately four times width at collar, smooth posteriorly, band not bottle shaped with sinuation of ventral margin and ventral groove not matched; pronotal disc with punctures on dorsal 0.5 - 0.75; discal pit obscure. Propleuron punctate posterolaterally. Mesoscutum with punctures obscure, relatively less so anteriorly than posteriorly; setae posteromedially directed near prescutellar furrow but posteriorly directed elsewhere, without line of setal convergence. Prescutellar furrow (fig. 24) straight medially, anterior margin delimited medially or not; cross carinae as high as scutellum or nearly so laterally, but carinae lower medially. Scutellum (fig. 25) with lunule narrower than costate area and with dorsal margin more convex medially than laterally; costate area with costae faint medially and anteriorly; anterior furrow wide, deep and smooth; dorsal groove shallow and narrow; dorsal margin of costate area with some surface irregularity on polished median part of scutellum; posterior margin of scutellum with distinct median lobe. Metanotum (fig. 27) laterally convex; posterior margin without rim; medial pit smooth, approximately parallel sided; lateral pits partly rugose and with smooth areas, wider than part of metanotum anterior to pit, without distinct anterior margin, part of metanotum anterior to pit smooth. Metapleuron (fig. 26) with median groove smooth, obsolete near midpit; slight sculpture on posterior 0.3 of posterior portion of metapleuron, but distinct punctures anterior to this; posteroventral carina rounded and slightly widened near hind coxa. Propodeum (fig. 27) with scattered shallow punctures basally, smooth or with slight rugose sculpture apically; spiracle oval, separated from pleural carina by less than its own least diameter; medioapical boss round, slightly thickened medially.

Tarsal claws shorter than width of apical tarsomere. Inner midtibial spur longer than outer and nearly as long as middle basitarsus. Inner and outer hindtibial spurs subequal in length and less than 0.5 as long as hind basitarsus. Hind coxa with punctures deep and distinct on most of surface (fig. 29).

Fore wing with 1Rs as long or longer than thickness of SC+R and inserted subbasally on parastigma; 2A absent; 3+4Rs slightly curved or straight, not decurved apically; 1Rs+M nearly straight. Hind wing with Cu+cu-a evenly curved or more curved near junction with M+Cu than near junction with 1A; SC+R at extreme base with convexity slightly protruded above upper plane of wing.*Metasoma*. T1 (fig. 28) slightly to moderately rugosopunctate lateroapically; apex narrower than base, with sides straight and apically convergent; apex moderately convex. T2 (fig. 28) with lateral margins sinuate; rugose laterally, polished medially; apical margin slightly sinuate. T3 with limited sculpture near furrow delimiting anterior margin; setae sparse; apex not desclerotized or whitened. T4 to T7 narrowly desclerotized, not whitened; setae scattered across each tergum, but sparse on T4. Islands elongate oval. Hypopygium (fig. 33) with setae absent midventrally at midlength; apex entire medioventrally. T9 approximately 1.8 times higher than wide (fig. 31). Second valvifer (fig. 31) extended into dorsal half of T9, apex rounded and anteriorly deflected. Third valvula (fig. 30) length 0.60 - 0.68 hind tibia length; setae on apical 0.75, concentrated apically but evenly distributed dorsoventrally; apex with triangular desclerotized area. Ovipositor (fig. 31) evenly and gradually decurved; approximately as long as hind tibia, with very slight subapical constriction; basal bulb not markedly set off from shaft.

Male. Unknown.

Cocoon, Larva. Unknown.

Hosts.— Reared from *Papilio zelicaon* Lucas by the Forest Insect Survey.

Phylogenetic Affinities.— *S. papilionae* is the sister species of *S. eugeni*.

Distribution.— Known only from the localities listed for type material (Fig. 141).

Chorological Affinities.— The range of this species apparently overlaps with those of *S. neomexicanus*, *S. circumflexus* and *S. masoni*, but *S. papilionae* is the only known Nearctic member of the *S. lateralis*-group. It is apparently allopatric with its sister species, *S. eugeni*.

Paratypes.— Two females, Cold Bay 163° W. Alaska 21-VIII 1952, W.R. Mason (CNC).

Sathon eugeni (Papp) 1972
(Figs. 34 - 44)

Apanteles eugeni Papp 1972: 336.
Apanteles magnicoxis Jakimavičius 1972: 306-308. Synonymy by Papp 1983: 260.
Apanteles fausta Nixon 1973: 177. Synonymy by Papp 1983: 260.
Sathon fausta; Mason 1981: 80.

Holotype.— Female, Hungarian Natural History Museum, Reg. No.2001.

Diagnosis.— **Female**. *Color*. Head and mesosoma piceous; metasoma piceous except for large fulvous area extended over most laterotergites and fulvous on apex of hypopygium, or entirely fulvous except rufopiceous to piceous terga; antenna light brown; fore and middle legs fulvous, hind leg with coxa piceous basally or entirely fulvous and apex of tibia and all tarsomeres darkened, rest of leg fulvous; third valvula rufopiceous to piceous.

Head. Clypeus with dorsal margin indistinct or completely effaced. Oral plate evenly pigmented, with dorsal margin flat but medially desclerotized (fig. 35).

Mesosoma. Pronotum with dorsal groove smooth or very slightly sculptured; ventral groove with slight foveolae (fig. 38). Mesoscutum with punctures obscure or absent over at least posterior 0.5. Scutellum (fig.

40) with costae faint medially and anteriorly, or absent except posteriorly and in dorsal groove; anterior groove deep, smooth, crossed by indistinct costae or costae absent; dorsal groove very narrow and shallow anteriorly; posterior margin of scutellum with marked median lobe. Metanotum with setae on sublateral lobe in some specimens (fig. 42). Propodeum with slightly to moderately developed punctures basally, rugose near medioapical boss (fig. 42).

Inner midtibial spur markedly longer than outer and nearly as long as middle basitarsus. Hind coxa with punctures faint on lateral surface (fig. 44).

Metasoma. T1 (fig. 43) smooth basally and in some specimens medially, punctate or rugosopunctate elsewhere; apex narrower than base, with sides straight. T2 (fig. 43) with lateral margins sinuate, but partially obscured by rugosity in some specimens; rugose, but with sculpture faint medially in some specimens; apical margin sligtly concave or nearly straight. T3 to T7 with apex desclerotized and slightly whitened. Hypopygium (fig. 36) with setae absent midventrally; apex immarginate. T9 approximately 2.25 times higher than wide (fig. 34). Second valvifer projected into upper 0.5 of T9, apex rounded and anteriorly deflected. Third valvula (fig. 34) with setae evenly distributed; apex with broad desclerotized area. Ovipositor (fig. 34) slightly decurved; approximately as long as hind tibia, without subapical constriction; basal bulb not markedly set off from shaft.

Male. Unknown.

Cocoon. Elongate oval, round in cross section, without flattened or slightly translucent sides; with thick strap of silk joined to cocoon by thinner web.

Larva (fig. 37). Solitary. Hypostoma with one large mandibular process and marked hypostomal spur; mandible blade curved at spex, with single row of straight, regular teeth on apical 0.5; silk press apparently with thin integument, only external details visible; labial sclerite wider than high.

Hosts.— *S. eugeni* has been reared from larvae of *Anthophila fabriciana* (L.) (Nixon 1973).

Phylogenetic Affinities.— *S. eugeni* is the sister species of *S. papilionae* new species.

Distribution.— Western part of the Palaearctic Region. Published records are from Sweden to Austria, and from England to the western U.S.S.R.

Chorological Affinities.— The range of this species overlaps with both other Palaearctic *Sathon* species. *S. eugeni* has been collected at sites where both *S. falcatus* and *S. lateralis* have been found, but is apparently allopatric with its Nearctic sister species, *S. papilionae*.

The *S. falcatus*-group

Adults of the *S. falcatus*-group are differentiated from those of the *S. lateralis*-group by the following combination of character states: costate area of scutellum with costae complete medially, although variably developed (figs. 47, 63, 70, 83, 96, 110, 124); propodeum in most specimens with at least trace of median carina at apex or with median carina distinct (figs. 49, 55, 72, 85, 98, 112, 126); T2 of metasoma with lateral margins obscured by rugosity or delimited by straight or slightly curved grooves, posterior margin nearly straight to markedly sinuate (figs. 50, 56, 73, 86, 99, 113, 127); T3 with setae absent in moderately sized mediobasal area; T6 and T7 uniformly sclerotized and pigmented across width, not emarginate; females with posterodorsal margin of hypopygium angulate (fig. 78) and/or sinuate (fig. 132) and third valvula decurved in most species (figs. 53, 64, 76, 89, 102, 116, 130); male (where known) with paramere truncate at apex and aedeagus triangular in cross section over part or all of length (figs. 66, 80, 93, 107, 122, 136).

Sathon laevidorsum new species
(Figs. 45 - 54)

Holotype.— Female, N. Cortez Pass, Mex., 10,000' 8-11-54. R.R. Dreisbach (CNC).

Derivation of Specific Epithet.— Latin, masculine, from 'laevis' meaning smooth and polished and 'dorsum'. It refers to the smoothness and general lack of sculpture, with the mesoscutal punctures obscure, the propodeum and T1 of the metasoma with little sculpture other than punctures and T2 of the metasoma medially smooth.

Diagnosis.— Adults of this species are differentiated from those of other *Sathon* species by the following combination of characters: propodeum and metasomal T1 polished, with sculpture other than punctures only at apex; metanotum with posterior margin rimulose laterally; base of SC+R of hind wing with inflated bulb protruded above upper plane of hind wing.

Description.— **Female.** *Color.* Head and mesosoma black; metasoma black with anterolateral fulvous spot; antennal scape piceous, slightly darker than flagellum; fore and middle legs fulvous with external surfaces of tibiae infuscate, hind leg with external surface and apex of tibiae and entire tarsi infuscate; third valvula piceous.

Head. Occiput narrowly and shallowly indented medially. Clypeus with dorsal margin obscure and ventral margin without reflexed rim. Face with median carina on upper 0.2. Malar space smooth near eye, but sculptured near mandibular articulation; furrow from ventral margin of eye to anterior mandibular articulation obscure.

Mesosoma. Pronotum (fig. 45) with dorsal groove indistinct, slightly arcuate and without foveolae; ventral groove with foveolae indistinct and without rugosity anteriorly; ventral margin moderately sinuate; width of ventral polished band at posteroventral angle greater than five times width at collar, smooth posteriorly, band not bottle shaped, with sinuation of ventral margin and ventral groove not matched; pronotal disc with few slight punctures over most of surface; discal pit moderately deep and distinct. Propleuron punctate posterolaterally. Mesoscutum with punctures obscure posteriorly, slightly less so anteriorly; setae posteriorly directed anteriorly and laterally, posteromedially directed medially and posteriorly, with line of setal convergence. Prescutellar furrow (fig. 46) straight medially, shallow, with anterior margin distinct; cross carinae as high as scutellum laterally, faint medially. Scutellum (fig. 47) with lunule as wide as costate area and with dorsal margin evenly convex; costate area without costae medially; anterior groove crossed by several costae; dorsal groove narrow; dorsal margin of costate area smooth; posterior margin of scutellum with indistinct median lobe. Metanotum (fig. 49) laterally convex; posterior margin with differentiated, granulate rim laterally but not medially; medial pit sculptured, with irregular sides; lateral pits moderately sculptured and with some smooth areas, approximately as wide as part of metanotum anterior to pit, without distinct anterior margin, part of metanotum anterior to pit smooth. Metapleuron (fig. 48) with median groove smooth and obscure near midpit; posterior portion of metapleuron with slight sculpture on posterior 0.33; posteroventral carina rounded and slightly widened near hind coxa. Propodeum (fig. 49) punctate basally, with slight, irregular rugosity apically; without raised carinae; spiracles oval, nearly in contact with pleural carina; medioapical boss round.

Tarsal claw slender, longer than width of apical tarsomere. Inner midtibial spur nearly twice as long as outer and nearly as long as middle basitarsus. Inner and outer hindtibial spurs subequal in length and less than 0.5 as long as hind basitarsus. Hind coxa with punctures moderately distinct (fig. 52).

Fore wing with 1Rs as long as thickness of SC+R and inserted basally on parastigma; 2A slight bulge on margin of 1A+2A; 3+4Rs very slightly sinuate, not decurved apically; 1Rs+M nearly straight. Hind wing with Cu+cu-a sinuate, markedly more curved near junction with M+Cu than at midlength and recurved near junction with 1A; SC+R at extreme base with bulb protruded above upper plane of wing (fig. 54).

Metasoma. T1 (fig. 50) smooth except for few punctures and slight lateral rugosity near apex; apex narrower than base, with sides sinuate; apex moderately convex. T2 (fig. 50) with lateral margins straight;

rugose laterally and smooth medially; apical margin sinuate. T3 smooth; apex with slightly wider desclerotized band than following terga. T4 to T7 slightly desclerotized, not whitened apically; setae evenly scattered across terga. Islands elongate oval to slit-shaped. Hypopygium (fig. 53) with setae evenly distributed; apex entire medioventrally; posterodorsal margin with slight sinuation. Third valvula (fig. 53) straight, with ventral margin sclerotized and convex; setae on apical 0.66 but sparse, slightly more concentrated on ventral half; apex with desclerotized area triangular, longer than wide and with sclerotized band parallel to, but separate from, ventral margin. Ovipositor (fig. 53) slightly and evenly decurved; slightly longer than hind tibia and with very slight subapical constriction; basal bulb not markedly set off from shaft.

Male, Larva, Cocoon. Unknown.

Hosts.— Unknown.

Phylogenetic Affinities.— *S. laevidorsum* is the sister species of *S. aggeris* .

Distribution.— Known only from the type locality (fig 141).

Chorological Affinities.— The range of this species does not overlap with any other *Sathon* species, and it is apparently allopatric with its sister species, *S. aggeris*. *S. laevidorsum* is the only known *Sathon* species from Central America.

Paratype.— Female, same data as holotype. Gold coated for S.E.M.

Sathon aggeris new species
(Figs. 55 - 67)

Holotype.— Female, Ecuador 3900m / Quito-Baeza Rd. / Elfin For. / Mar. '79 W. Mason (CNC).

Derivation of Specific Epithet.— Latin, masculine, meaning heap or mound and referring to the unusually protuberant convexity of the first tergum of the metasoma in the female.

Diagnosis.— Adults of this species are differentiated from those of other *Sathon* species by the following combination of character states: first tergum of the metasoma very convex, especially in the female where it is developed into a tubercle; posterior margin of metanotum with a differentiated, foveolate rim; hind wing with SC+R with an enlarged tubercle protruded markedly above upper plane of wing.

Description.— **Female.** *Color*. Head and mesosoma black with metallic blue highlights; metasoma black, with apical terga and hypopygium piceous, and lateral white stripe on laterotergites and dorsal margins of sternites which blends with black of terga and sternites and is narrowed posteriorly; antenna piceous; fore and middle legs fulvous and with apex of femora, external surfaces of tibiae and entire tarsi piceous, hind leg as other legs but also with trochanters and coxae black; third valvula piceous.

Head. Occiput narrowly and shallowly indented medially. Clypeus with dorsal margin obscure and ventral margin without reflexed rim. Face with median carina on upper 0.2. Malar space with few scattered punctures, otherwise smooth; furrow from ventral margin of eye to anterior mandibular articulation absent except near eye.

Mesosoma. Pronotum (fig. 61) with dorsal groove straight and without foveolae; ventral groove with foveolae indistinct and without rugosity anteriorly; ventral margin moderately sinuate; width of ventral polished band at posteroventral angle more than five times width at collar, striate posteriorly, band not bottle shaped, sinuation of ventral margin and ventral grooved not matched; pronotal disc with few slight punctures on dorsal 0.33 of surface; discal pit moderately deep and .distinct. Propleuron striate posterolaterally. Mesoscutum with punctures obscure posteriorly, slightly less so anteriorly; setae posteriorly directed on anterior half, posteromedially directed on posterior half, but without line of setal convergence. Prescutellar furrow (fig. 62) straight, with anterior margin merged with mesoscutum and obscure; cross carinae lower than scutellum and indistinct in some specimens. Scutellum (fig. 63) with lunule as wide as costate area and with dorsal margin evenly convex; costate area without costae medially; anterior furrow crossed by numerous distinct costae; dorsal groove extremely shallow; dorsal margin of costate area smooth; posterior margin of scutellum with slight median lobe. Metanotum (fig. 55) laterally convex; posterior margin with differentiated, foveolate rim; medial pit sculptured, straight sided; lateral pits robustly and entirely sculptured, wider than part of metanotum anterior to pit, with distinct anterior margin, part of metanotum anterior to pit smooth. Metapleuron with median groove smooth and obsolete near midpit; slight sculpture on posterior 0.5 of posterior portion of metapleuron; posteroventral carina angulate and notably widened near hind coxa. Propodeum (fig. 55) areolate-rugose with lateroapical rugose tubercles; raised carinae absent; spiracle oval, nearly in contact with pleural carina; medioapical boss round.

Tarsal claws slender, longer than width of apical tarsomere. Inner midtibial spur nearly twice as long as outer and nearly as long as middle basitarsus. Inner hindtibial spur slightly longer than outer and more than 0.5 as long as hind basitarsus. hind coxa with punctures on hind coxa indistinct on lateral surface, distinct on dorsal surface (fig. 58).

Fore wing with 1Rs nearly as long as thickness of SC+R and inserted subbasally on parastigma; 2A lightly pigmented trace visible almost to posterior wing margin; 3+4Rs slightly sinuate, slightly decurved apically; 1Rs+M sinuate. Hind wing with Cu+cu-a sinuate, markedly more curved near junction with M+Cu than at midlength and recurved near junction with 1A; SC+R at extreme base with bulb protruded above upper plane of wing (fig. 67).

Metasoma. T1 (fig. 56) rugose; apex wider than base, with sinuate sides; apex with very convex tubercle (fig 57). T2 (fig. 56) with lateral margins straight; rugose apically and longitudinally rugose basally; apical margin slightly sinuate. T3 sculptured at extreme base; apex desclerotized and whitened. T4 to T7 slightly desclerotized, not whitened apically; setae limited to apical half of each tergum, in form of single row medially. Island oval on laterotergum 3, progressively elongate posteriorly to slit-shaped on laterotergum 6. Hypopygium (fig. 64) with setae absent midventrally at midlength; apex entire medioventrally; posterodorsal margin sinuate and with slight lobe. Third valvula (fig. 64) straight, ventral margin extensively desclerotized and convex; setae on apical 0.66, concentrated on ventral half; apex with narrow, acute desclerotized area. Ovipositor (fig. 64) nearly straight; approximately as long as hind tibia; without subapical constriction; basal bulb not markedly set off from shaft.

Male. Similar to female, except: maxilla and labium brown; coxa piceous; tibiae, tarsi and entire hind leg rufopiceous except for piceous internal and external surfaces of femora and external surfaces of rest of leg; clypeus 2.0 as wide as high in some specimens; face with median carina obscure; eye with posterior margin convex; pronotum with few faint foveolae in dorsal groove; ventral polished band with few faint striae in most specimens; prescutellar furrow with cross carinae low but not faint; scutellar costate area with costae complete, both dorsal and anterior grooves slightly impressed; metanotum (fig. 59) with medial pit widened anteriorly and lateral pits without distinct anterior margin and extended nearly to anterior margin of metanotum; propodeum (fig. 59) without tubercles, rugosity low and with some smooth areas basally and lateroapically in some specimens; fore wing with 2A faint bulge on 1A+2A, 1Rs+M evenly curved; hind wing with 2A evenly curved; T1 of metasoma (figs. 59, 60) narrowed apically, areolate rugose to rugose and markedly convex but without medioapical tubercle; T2 of metasoma (fig. 60) with lateral grooves indistinct in some specimens, sculpture punctate or rugose; paramere obliquely truncate, narrow anteroventrally, narrower at apex than at base, length much less than 0.33 of metasoma (fig. 66); aedeagus triangular in cross section and slightly knobbed at apex but flattened at base (fig. 66); digitus short, apex scarcely longer than broad (fig. 66). Basal ring medially desclerotized, without median carinae (fig. 65).

Sathon aggeris is an unusually dimorphic species, with males more different from the female than some other *Sathon* species are from one another. However, the paratype males do have the autapotypies for the species, the completely rimulose posterior margin of the metanotum and the markedly convex T1 of the metasoma (although much less developed than the female).

Cocoon, Larva. Unknown.

Hosts.— Unknown.

Phylogenetic Affinities.— *S. aggeris* is the sister species of *S. laevidorsum* .

Distribution.— Known only from the type locality (fig. 141).

Chorological Affinities.— The range of this species does not overlap with any other *Sathon* species. This species is the only known South American *Sathon*. It is not known if *S. aggeris* is sympatric with its Central American sister species, *S. laevidorsum*.

Paratypes.— Four males, same data as holotype, one gold coated for S.E.M.

Sathon masoni new species

(Figs. 68 - 80)

Holotype.— Female, Anchorage, Alaska / 24-VII-1951. / R.S. Bigelow. [with det. label, Apanteles n. sp. falcatus / Det. W.R.M. Mason 74.] (CNC).

Derivation of Specific Epithet.— Named with pleasure for W.R.M. Mason, who first recognized this new species, and without whose guidance and pioneering work this study of *Sathon* could not have been done.

Diagnosis.— Adults of this species are differentiated from those of other *Sathon* species by the following combination of character states: propodeum with raised lateroapical carinae and rugosity; antennal scape concolorous with flagellum; hypopygium of female with angulate posterodorsal margin; apex of ovipositor of female with well developed subapical constriction.

Description.— **Female.** *Color.* Head and mesosoma piceous; metasoma piceous with anterolateral fulvous or brown spot; antenna fulvous basally in some specimens; fore and middle legs fulvous and darkened apically, hind leg fulvous, darkened apically and with base of coxa piceous; third valvula piceous.

Head. Occiput narrowly and shallowly indented medially and less convex dorsally than laterally. Clypeus with dorsal margin distinct and ventral margin with rim absent or medially obscure. Face with short median carina on dorsal 0.30. Malar space with sculpture posteriorly from eye to mandible or only near mandible; groove from ventral margin of eye to anterior mandibular articulation medially or almost entirely obsolete. Oral plate evenly pigmented, dorsal margin slightly convex (fig. 77).

Mesosoma. Pronotum (fig. 68) with dorsal groove decurved and moderately foveolate; ventral groove foveolate posteriorly and broadly foveolate anteriorly, but not rugose; ventral margin sinuate; width of ventral polished band at posteroventral angle approximately four times width at collar, smooth posteriorly, not bottle shaped with sinuation of ventral groove and ventral margin not matched; pronotal disc with punctures over most of surface; discal pit obscure. Propleuron punctate posterolaterally. Mesoscutum with posterior edge of each puncture obscure, but relatively more distinct on anterior part of mesoscutum than posterior part; setae posteriorly directed anteriorly and laterally, posteromedially directed medially and posteriorly, with line of setal convergence. Prescutellar furrow (fig. 69) arcuate or irregular, but not straight, with anterior margin distinct; cross carinae nearly as high as scutellum and median carina highest in most specimens. Scutellum (fig. 70) with lunule narrower than costate area and with dorsal margin evenly convex or slightly more convex medially than laterally; costate area with costae complete, in most specimens with irregular carina extended across costae and parallel to anterior and dorsal grooves, or at least with some irregular carination between some costae; anterior groove crossed by several costae; dorsal groove wide; dorsal margin of costate area in most specimens with some sculpture or surface irregularity on polished median part of scutellum; posterior margin of scutellum with moderate median lobe. Metanotum (fig. 72) slightly convex laterally; posterior margin without rim; medial pit sculptured, narrowed apically; lateral pits partially sculptured, wider than part of metanotum anterior to pits, without distinct anterior margin, part of metanotum anterior to pit smooth. Metapleuron (fig. 71) with foveolae of median groove indistinct or absent, furrow distinct, but obsolete near midpit in some specimens; posterior part of metapleuron with slight sculpture on posterior 0.33, but with indistinct granular microsculpture anterior to this; posteroventral carina rounded and slightly widened near hind coxa. Propodeum (fig. 72) punctate basally, rugose apically, with raised lateroapical carinae and rugosity; median carina on apical 0.5, with irregular surface that confluent with transverse rugosity on median propodeal area; spiracle round, separated from pleural carina by 0.5 or more of its own diameter; medioapical boss round, but with median carina widened apically in some specimens and boss appearing triangular.

Tarsal claws stout, shorter than width of apical tarsomere. Inner midtibial spur slightly longer than outer and approximately 0.75 as long as middle basitarsus. Inner and outer hindtibial spurs subequal in length and less than 0.5 as long as hind basitarsus. Hind coxa with punctures in longitudinal band on lateral surface and distinct on dorsal surface, but some specimens with all punctures indistinct (fig. 74).

Fore wing with 1Rs longer than thickness of SC+R and inserted subbasally on parastigma; 2A slight knob on 1A+2A, but some specimens with unpigmented trace visible part way to wing margin; 3+4Rs slightly sinuate, not decurved apically; 1Rs+M evenly slightly curved. Hind wing with Cu+cu-a moderately curved near junction with M+Cu and straight near junction with 1A; SC+R at extreme base with convexity slightly protruded above upper plane of wing.

Metasoma. T1 (fig. 73) rugosopunctate lateroapically, polished medially in most specimens but rugose in markedly sculptured specimens; apex narrower than base, with sides straight and apically convergent; apex moderately convex. T2 (fig. 73) with lateral margins obscured by rugosity; rugose, but with polished median area; apical margin sinuate, but furrow marking margin incomplete in some specimens. T3 smooth; apex not desclerotized or whitened. T4 to T7 not desclerotized or whitened; setae scattered evenly across terga. Island oval or teardrop-shaped. Hypopygium (fig. 78) with setae concentrated basally and apically, or absent midventrally at midlength; apex entire medioventrally; posterodorsal margin angulate and joined to ventral margin at approximately 80°, in some specimens also slightly sinuate near apex. T9 approximately 2.5 times higher than wide (fig. 76). Second valvifer (fig. 76) short, barely projected into upper 0.5 of T9, apex in form of narrow bottleneck that has apodemes anteriorly and posteriorly. Third valvula (fig. 76) decurved, with ventral margin sclerotized and concave, but only slightly concave in some specimens; setae on apical 0.75 or more, only slightly more concentrated ventrally than dorsally; apex with desclerotized area small and acute or absent. Ovipositor (fig. 76) evenly shallowly decurved; slightly longer than hind tibia, with subapical constriction; basal bulb somewhat abruptly set off from shaft.

Male. Similar to female, except: some specimens with mesoscutal punctures evenly delimited on all sides, but punctures as a whole less distinct posteriorly than anteriorly; dorsal margin of scutellar costate area irregular in some specimens; metanotum without lateral convexity; penultimate fore tarsomere approximately 1.8 times long as wide; paramere obliquely truncate, narrow anteroventrally, slightly widened at apex and approximately as wide as extreme base, length much less than 0.33 of metasoma (fig. 80); aedeagus triangular in cross section throughout length and distinctly knobbed at apex (fig. 80); digitus slightly elongate (fig. 80); basal ring medially desclerotized, without median carinae (fig. 79).

Cocoon, Larva. Unknown.

Hosts.— Unknown.

Phylogenetic Affinities.— *S. masoni* is the sister species of *S. cinctiformis* .

Distribution.— Northwestern in Nearctic Region. I have examined specimens from the following territory and states: **Canada**. North West Territories. **United States**. Alaska, Idaho, Minnesota (fig 141).

Chorological Affinities.— The range of this species overlaps with that of *S. neomexicanus* and it has been collected at some of the same sites, but is apparently not sympatric with its sister species *S. cinctiformis*. Paucity of specimens outside of Alaska shows lack of knowledge of true southern extent of range and species status of southern specimens.

Paratypes.— 5 females, 2 males, same data as holotype. 12 females, male, Unalakleet, Alaska, 5-14-VIII-61 B.S. Heming(CNC). 9 females, male, Unalakleet, Alaska, 2-29-VIII-61 R. Madge (CNC). 22 females, Big Delta Alaska, 13-VII-1951 J.R. McGillis (CNC). 7 females, Shaw Crk. Alaska, m. 289 Rich Hwy, 11-VII-1951 Mason & McGillis (CNC). 2 females, Birch L. Alaska, near Fairbanks, 7-VII-1951 W.R.M. Mason (CNC). 2 females, Paxson Lodge Gulkana, Alaska, 4-VIII-1951 W.R.M. Mason (CNC). 2 females, King Salmon, Naknek R. Alaska, 8-VIII-1952 J.B. Hartley (CNC). 3 females, King Salmon, Naknek R. Alaska, 11-31-VIII 1952 W.R.M. Mason (CNC). 2 females, Mt. McKinley 3500', VIII-7-54

Alaska, David Townes (AEI). female, Mt. McKinley N. Pk. Alaska, F.W. Morand, Coll. 1932 (USNM). 4 females, Mile 272 Alaska, Richard Hwy 26-VIII-1951 W.R.M. Mason (CNC). female, Coleburn Ida. Bonner Co., VI-23-60 A.R. Gittins Collector (USNM). 2 females, Eaglesnest, Minn. Aug. 4 1958 collected by W.V. Balduf (USNM). female, Fort Simpson N.W.T. 15-VIII-1950 D.P. Whillans (CNC).

Sathon cinctiformis (Viereck) 1911

(Figs. 81 - 93)

Apanteles (Protapanteles) cinctiformis Viereck 1911: 176.
Apanteles cinctiformis; Muesebeck 1921: 526.
Sathon cinctiformis; Mason 1981: 80.
Apanteles cinctiformis sensu Cole 1931 and Claassen 1921 = *Lathrapanteles papaipemae sensu* Williams 1985.

Type Material Examined.— Holotype: U.S.N.M. Cat. No. 13502. Great Falls, Virginia, June 18; collected by Nathan Banks.

Diagnosis.— Adults of this species are differentiated from those of other *Sathon* species by the following combination of character states: scape fulvous, lighter in color than flagellum; propodeum with lateroapical rugose tubercles or raised carinae; T1 of the metasoma markedly rugose, even in mediobasal groove.

Description.— **Female.** *Color.* Head and mesosoma rufopiceous to piceous; metasoma piceous on T1 and apical terga, fulvous elsewhere, but terga darker than sterna in some specimens; antennal scape fulvous, flagelum brown; legs and third valvula fulvous.

Head. Occiput narrowly and shallowly indented medially, dorsal area concave in some specimens. Clypeus with dorsal margin obscure or slightly marked and ventral margin with reflexed rim present laterally or completely. Face with median carina on dorsal 0.4. Malar space with slightly or moderately developed sculpture near mandible; groove from ventral margin of eye to anterior mandibular articulation obscure over most of length or absent except near eye. Oral plate evenly pigmented, dorsal margin flat (fig. 90).

Mesosoma. Pronotum (fig. 81) with dorsal groove slightly to markedly decurved and foveolate; ventral groove foveolate posteriorly and with rugosity anteriorly, rugosity indistinct in some specimens; ventral margin sinuate; width of ventral polished band at posteroventral angle approximately four times width at collar, smooth posteriorly, band bottle shaped with sinuation of ventral margin and ventral groove matched, but dorsal margin of band irregular anterior to midlength; pronotal disc with punctures over most of surface; discal pit deep. Propleuron with punctures obscure posterolaterally. Mesoscutum with posterior edge of most punctures obscure, punctures almost absent posteriorly and distinct anteriorly, some specimens with punctures distinct all around; setae posteromedially directed near prescutellar furrow, posteriorly directed elsewhere, without line of setal convergence. Prescutellar furrow (fig. 82) arcuate, with anterior margin distinct; cross carinae as high as scutellum or nearly so laterally, but carinae lower medially. Scutellum (fig. 83) with lunule as wide as costate area and with dorsal margin evenly convex; costate area with costae complete or faint medially, with carina parallel to anterior and dorsal grooves, or at least with some irregular carination between some costae; anterior furrow moderately deep and crossed by several costae; dorsal groove wide; dorsal margin of costate area with some sculpture or irregularity present on polished median part of scutellum; posterior margin of scutellum with slight median lobe. Metanotum (fig. 85) slightly convex laterally; posterior margin without rim; medial pit sculptured, with irregular anteriorly divergent sides; lateral pits slightly rugose with smooth areas to almost completely rugose, approximately as wide or narrower than part of metanotum anterior to pit, with distinct anterior margin, part of metanotum anterior to pit sculptured. Metapleuron (fig. 84) with median groove distinct, foveolate except near midpit; posterior part of metapleuron with marked rugose and granular sculpture on posterior 0.4 - 0.8 and with one or several carinae as high as posterior carina and protruded on to sculptured area; posteroventral carina rounded and slightly widened near hind coxa. Propodeum (fig. 85) punctate basally, rugose apically and with raised carinae and rugosity lateroapically; median carina on apical 0.6 - 0.9, with irregular surface confluent with slight transverse rugosity on median propodeal area; spiracle round or broadly oval, separated from pleural carina by its own diameter, but connected to pleural carina by carina of equal height in some specimens; medioapical boss round, but some specimens angularly connected to median carina and appearing somewhat broadly triangular.

Tarsal claws stout, shorter than width of apical tarsomere. Inner midtibial spur slightly longer than outer and nearly 0.75 as long as middle basitarsus. Inner and outer hindtibial spurs subequal in length and less than 0.5 as long as hind basitarsus. Hind coxa with punctures obscure except for narrow longitudinal band on lateral surface and deep punctures on dorsal surface, but some specimens with punctures indistinct (fig. 87).

Fore wing with 1Rs longer than thickness of SC+R and inserted subbasally on parastigma; 2A slight bulge on 1A+2A; 3+4Rs slightly sinuate, not decurved apically; 1Rs+M straight. Hind wing with Cu+cu-a moderately curved near junction with M+Cu and nearly straight near junction with 1A; SC+R at extreme base with convexity slightly protruded above upper plane of wing.

Metasoma. T1 (fig. 86) striate-rugose medially and rugose or areolate-rugose apically and laterally; apex narrower than base, but wider subapically than base in some specimens, with sides sinuate, or straight and parallel on basal 0.75 but apically convergent on apical 0.25; apex slightly convex. T2 (fig. 86) with lateral margins obscured by rugosity; rugose, but with slight granular sculpture medially in some specimens; apical margin slightly sinuate to almost straight. T3 rugose mediobasally, sculptured area small in some specimens; apex slightly desclerotized and whitened. T4 to T7 slightly desclerotized, not whitened; setae evenly scattered across terga, but limited to a single row on T4 in some specimens. Islands oval to elongate oval. Hypopygium (fig. 91) with setae absent or scarce midventrally at midlength; apex entire medioventrally; posterodorsal margin angulate and slightly sinuate near apex, joined to ventral margin at approximately 80°. T9 approximately 2.0 times higher than wide (fig. 89). Second valvifer (fig. 89) short, barely projected into upper 0.5 of T9, apex slightly narrowed and with irregular margin dorsally. Third valvula (fig. 89) decurved, with ventral margin sclerotized and concave over most of length; setae on apical 0.75, evenly distributed, bent tipped near apex; apex with desclerotized area triangular and emarginate at tip. Ovipositor (fig. 89) nearly straight basally but sharply decurved at apical 0.3 and nearly straight distal to that; slightly longer than hind tibia, without subapical constriction; basal bulb somewhat abruptly set off from shaft.

Male. Similar to female, except: metasoma with more apical terga and some sternites rufopiceous to piceous, scape piceous or basal half of flagellum fulvous with scape and flagellum concolorous in some specimens; metapleuron with foveolae of median groove indistinct except near base, sculpture of posterior portion of metapleuron slightly to moderately developed and present only on 0.4 of posterior part; propodeal spiracle oval and separated from pleural carina by less than its own diameter; T1 apically narrowed throughout length in some specimens; paramere obliquely truncate, narrow anteroventrally, apex slightly widened and slightly narrower than extreme base, length much less than 0.33 of metasoma (fig. 93); aedeagus triangular in cross section throughout length and distinctly knobbed at apex (fig. 93); digitus slightly elongate (fig. 93); basal ring medially desclerotized and without median carinae (fig. 92).

Cocoon, Larva. Unknown.

Host.— Unknown.

Phylogenetic Affinities.— *S. cinctiformis* is the sister species to *S. masoni.*

Distribution.— Eastern Nearctic. I have examined specimens from the following provinces and states: **Canada**. Ontario, Quebec. **United States**. Indiana, Iowa, Maryland, Michigan, New Jersey, New York, North Carolina, Ohio, Pennsylvania, Rhode Island, Vermont, Virginia, Wisconsin (fig. 141).

Chorological Affinities.— The range of this species overlaps broadly with that of *S. neomexicanus*, but it is apparently not sympatric with its primarily western sister species, *S. masoni.*

Sathon circumflexus new species

(Figs. 94 - 107)

Holotype.— Female, Doolittle Ranch / 9800' Mt. Evans / Colo. 10-VII B.H. Poole [50 km. S.W. Denver in Clear Creek CO.] (CNC).

Derivation of Specific Epithet.— Latin, masculine, meaning curved or flexed and refering to the arc-like and markedly decurved ovipositor.

Diagnosis.— Adults of this species are differentiated from those of other *Sathon* species by the following combination of character states: propodeal boss thickened medially; female with ovipositor evenly decurved and semicircular; male with paramere apex wider than base and length slightly less than 0.33 of metasoma.

Description.— **Female.** *Color.* Head and mesosoma piceous; metasoma piceous with anterolateral fulvous spot; antenna piceous; fore and middle legs fulvous, hind leg fulvous with coxa, apex of tibia, tarsi and in some specimens external surface of femur rufopiceous; third valvula piceous.

Head. Occiput broadly and shallowly indented medially (fig. 105). Clypeus with dorsal margin delimited laterally, but slightly less so medially, ventral margin with very slight reflexed rim. Face with median carina on upper 0.25. Malar space sculptured posteriorly near mandible; furrow from ventral margin of eye to anterior mandibular articulation complete but indistinct, to absent near mandible. Oral plate with mediolateral pigment lines, dorsal margin convex (fig. 103).

Mesosoma. Pronotum (fig. 94) with dorsal groove straight and smooth or with few foveolae; ventral groove narrow, with foveolae faint in some specimens and without rugosity anteriorly; ventral margin sinuate; width of ventral polished band at posteroventral angle approximately five times width at collar, striate posteriorly, band bottle-shaped with sinuation of ventral margin and ventral groove matched; pronotal disc with punctures on most of surface; discal pit obscure. Propleuron with slight punctures laterally. Mesoscutum with punctures obscure; setae posteriorly directed and without line of setal convergence, but some specimens with setae posteromedially directed on notauli or posterior part of mesoscutum and then line of setal convergence present in broad, indistinct form. Prescutellar furrow (fig. 95) arcuate, shallow, with anterior margin indistinct medially in some specimens; cross carinae as high as scutellum laterally, but lower or absent medially. Scutellum (fig. 96) with lunule almost as wide as costate area and with dorsal margin slightly more convex medially than laterally, or irregular; costate area without costae medially; anterior groove crossed by several costae; dorsal groove indistinct over most of length; dorsal margin of costate area with foveolae of dorsal groove impressed in some specimens; posterior margin of scutellum with slight median lobe. Metanotum (fig. 98) laterally convex; posterior margin without rim; medial pit nearly smooth, straight sided; lateral pits entirely sculptured or with small smooth areas near medial pit, wider than part of metanotum anterior to pit, without distinct anterior margin, part of metanotum anterior to pit smooth. Metapleuron (fig. 97) with median groove slightly foveolate, obsolete or distinct near midpit; posterior portion of metapleuron with slight sculpture on posterior 0.5 or less; posteroventral carina rounded and slightly widened near hind coxa. Propodeum (fig. 98) punctate basally, with few wrinkles apically; median carina irregular trace near medioapical boss, but extended toward metanotum by a band of low rugosity in some specimens; spiracle oval, separated from pleural carina by its own least diameter, but connected to pleural carina by raised area as high as carina, raised area and carina low in some specimens; medioapical boss round, thickened medially.

Tarsal claws stout, shorter than width of apical tarsomere. Inner midtibial spur slightly longer than outer and 0.75 as long as middle basitarsus. Inner and outer hindtibial spurs subequal in length and less than 0.5 as long as hind basitarsus. Hind coxa with punctures obscure, less so dorsally than laterally (fig. 100).

Fore wing with Rs base as long or longer than thickness of SC+R and inserted subbasally on parastigma; 2A slight convexity on 1A+2A; 3+4Rs straight or slightly curved, not decurved apically; 1Rs+M straight. Hind wing with Cu+cu-a curved near junction with M+Cu and straight near junction with 1A; SC+R at extreme base with convexity slightly protruded above upper plane of wing.

Metasoma. T1 (fig. 99) smooth basally and medioapically, but rugose lateroapically and with few punctures in some specimens; apex narrower than base, sides slightly sinuate; apex moderately convex. T2 (fig. 99) with lateral margins straight or slightly concave; rugose laterally and with faint granular microsculpture at base; apical margin sinuate. T3 smooth; apex slightly desclerotized and whitened. T4 to T7 scarcely desclerotized, not whitened apically; setae evenly scattered across terga. Islands oval. Hypopygium (fig. 104) with setae absent midventrally except near apex; apex entire medioventrally; posterodorsal margin sinuate. T9 approximately 2.5 times higher than wide (fig. 102). Second valvifer (fig. 102) projected into upper 0.5 of T9, apex slightly expanded dorsal to point of third valvula attachment and with apodeme posteriorly. Third valvula (fig. 102) decurved, with ventral margin sclerotized and concave over most of length; setae on almost all of length, but concentrated apically and ventrally; apex with divided triangular desclerotized area. Ovipositor (fig. 102) evenly but markedly decurved over entire length; longer than hind tibia, without subapical constriction; basal bulb abruptly set off from shaft.

Male. Similar to female, except: foveolae of pronotal grooves almost absent in some specimens; cross carinae of prescutellar furrow equally distinct medially and laterally in some specimens; penultimate fore tarsomere approximately 2.0 times long as wide; T1 of metasoma (fig. 101) with sides nearly straight; T2 much longer than wide at apex, with granular microsculpture obscure at base; paramere obliquely truncate, narrow anteroventrally, wider at apex than at base, length slightly less than 0.33 of metasoma (fig. 107); aedeagus triangular in cross section throughout length and distinctly knobbed at apex (fig. 107); digitus elongate (fig. 107); basal ring evenly sclerotized, with slender median carina (fig. 106).

Cocoon, Larva. Unknown.

Hosts.— Unknown.

Phylogenetic Affinities.— *S. circumflexus* is the sister species to *S. neomexicanus* + *S. falcatus*.

Distribution.— Southwestern United States. I have examined specimens from the following states: **United States**: Arizona, Colorado, New Mexico (fig. 141).

Chorological Affinities.— The range of this species overlaps with *S. neomexicanus* and specimens of both species have been collected at some of the same localities, at the same time.

Paratypes.— 11 females, 2 males, Doolittle Ranch, 9800' Mt. Evans, Colo. 10-VII Collectors B.H. Poole, S.M. Clark and W.R.M. Mason '61 (CNC). Female, male, Doolittle Ranch, Mt. Evans Colo. 31-VII-1961 C.H. Mann 10,000'(CNC). 5 females, Loveland Pass W. slope 9850' 8-VIII-1961 COLO. B.H. Poole (CNC). 12 females, male, Chicago Cr. 8800' Clear Cr. Co. COLO. Aug 2, 5 and 25 Collectors B.H. Poole and C.H. Mann '61 (CNC). 4 females, West Chicago Cr. 9800' Clear Cr. Co. COLO. 11-VIII-1961 Collectors B.H. Poole and S.M. Clark (CNC). Female, Echo L. 9600' Mt. Evans COLO. July 26 1961 B.H. Poole (CNC). Female, Cameron Pass, COLO. August 18 1940, Elev. 9850ft. C.W. Sabrosky Collector (UM) 2 females, Colo. 2012 [Grizzley Creek, Lar. Co. 7-19-96] Collection C.F. Baker (USNM). Female, Colo. 2013 [Forresters Ranch. 8-3-96] Collection C.F. Baker (USNM). Female, Colo. 2061 [Hardys Ranch, North Park. 7-29-96] Collection C.F. Baker (USNM). Female, Colo. 1547 [Fort Collins. 6-7-95] Collection C.F. Baker (USNM). Female, Ariz. 2569 [San Francisco Mts., Flagstaff. 7-23-97] Collection C.F. Baker (USNM). Female, Ariz. Graham Co. Hospital Flat Pinaleno Mts. Alt. 8950' 2-VIII-1965 Hugh B. Leech (CAS). Female, Chiricahua Mts. Rustlers Park VIII-16-74 Ariz. H.&M. Townes (AEI). Female, Cimarron, N. Mex. VIII 23 '55 9500' David Townes (AEI).

Sathon neomexicanus (Muesebeck) 1921 (1920)
(Figs. 108 - 121)

Apanteles neomexicanus Muesebeck 1921 (1920): 529.

Apanteles caudatus Muesebeck 1922: 16. Synonymy by Muesebeck and Walkley 1951: 131.

Sathon neomexicanus; Mason 1981: 78.

Type Material Examined.— *A. neomexicanus* - Holotype: U.S.N.M. Cat. No. 22528, Santa Fe, New Mexico. Collected by T.D.A. Cockerell, August 14, 1895. Paratypes: 3 females, same data as Holotype. Female, Colo. 2158, Coll C.F. Baker.

A. caudatus - Paratypes: Male, Carbonate, Columbia Riv. Br. Col. Jy 7-12 '08, Alt 2600 ft. J.C. Bradley (Cornell U. Cat. No. 568.4, USNM Cat. No. 24330).

Female, Mica, WASH 14 July 1918, A.L. Melander.

Diagnosis.— Adults of this species are differentiated from those of other *Sathon* species by the following combination of character states: occiput narrowly and shallowly indented medially; propodeum smooth or with slight irregular rugosity, median carina in form of short trace or extended over most of propodeal length; 3+4Rs of fore wing slightly sinuate, markedly decurved near wing apex; T1 of metasoma with straight, nearly parallel sides and wide medioapical smooth area; female with ovipositor markedly longer than hind tibia; male with enlarged genital capsule, length more than depth of metasoma.

Description.— **Female.** *Color.* Head and mesosoma piceous; metasoma piceous with anterolateral fulvous spot, or almost entirely fulvous except for T1, margins of T2, and apex of T9; antenna piceous; foreleg fulvous or with coxa piceous near base, middle leg fulvous or with coxa piceous near base, and hind leg fulvous with coxa piceous on basal 0.33 or more; third valvula piceous.

Head. Occiput narrowly and shallowly indented medially (fig. 1). Clypeus with dorsal margin indistinct in some specimens, ventral margin without reflexed rim. Face with median carina on dorsal 0.33, some specimens with indistinct polished ridge on middle 0.33. Malar space sculptured posteriorly and with furrow from ventral margin of eye to anterior mandibular articulation complete, or sculptured over most of surface and groove obscured. Oral plate with mediolateral pigment lines, dorsal margin concave (fig. 117).

Mesosoma. Pronotum (fig. 108) with dorsal groove straight or slightly decurved and moderately foveolate; ventral groove foveolate throughout length, but with little or no rugosity anteriorly; ventral margin sinuate; width of ventral polished band at posteroventral angle four to five times width at collar, smooth posteriorly, band bottle shaped with sinuation of ventral margin and ventral groove matched; pronotal disc with punctures over most of surface; discal pit obscure to moderately deep and distinct. Propleuron punctate posterolaterally. Mesoscutum with punctures absent or indistinct posteriorly, distinct anteriorly; setae posteromedially directed on notauli and near prescutellar furrow, posteriorly directed elsewhere, line of setal convergence short or absent. Prescutellar furrow (fig. 109) arcuate or nearly straight medially, with anterior margin indistinct medially; cross carinae as high as scutellum or nearly so laterally, but carinae lower medially. Scutellum (fig. 110) with lunule as wide as costate area and with dorsal margin slightly more convex medially than laterally, or irregular; costate area with costae complete, with irregular cross carinae in some specimens; anterior groove crossed by several to numerous costae, dorsal groove absent or indistinct; dorsal margin of costate area smooth; posterior margin of scutellum with slight or no median lobe. Metanotum (fig. 112) slightly convex laterally; posterior margin without rim; medial pit nearly smooth, with straight or slightly curved but anteriorly divergent sides; lateral pits rugose but with smooth areas, as wide as or narrower than part of metanotum anterior to pit, with distinct anterior margin, part of metanotum anterior to pit sculptured in some specimens. Metapleuron (fig. 111) with median groove slightly sculptured but distinct over entire length; posterior part of metapleuron with deep punctures on entire length of surface, at least on dorsal 0.5; posteroventral carina rounded and slightly widened near hind coxa. Propodeum (fig. 112) punctate basally, with slightly developed wrinkles apically; median carina irregular trace near medioapical boss or extended over most of propodeal length; spiracle broadly oval, separated from pleural carina by less than its own least diameter; medioapical boss round.

Tarsal claws stout, shorter than width of apical tarsomere. Inner midtibial spur slightly longer than outer and approximately 0.75 as long as middle basitarsus. Inner and outer hindtibial spurs subequal in length and less than 0.5 as long as hind basitarsus. Hind coxa with punctures obscure except for longitudinal band on lateral surface, distinct on dorsal surface (fig. 114).

Fore wing with 1Rs as long or longer than thickness of SC+R and inserted subbasally on parastigma; 2A slight decurvature or bulge on 1A+2A and unpigmented crease; 3+4Rs slightly sinuate, decurved apically; 1Rs+M slightly curved, or in some specimens slightly sinuate. Hind wing with Cu+cu-a moderately curved near junction with M+Cu, straight or slightly decurved near junction with 1A; SC+R at extreme base with convexity slightly protruded above upper plane of wing.

Metasoma. T1 (fig. 113) slightly rugose apically and with medioapical smooth area on middle 0.33 to 0.75; apex slightly narrower than base, with sides sinuate or slightly curved at apex; apex moderately convex, but smooth area slightly concave in some specimens. T2 (fig. 113) with lateral margins slightly curved; rugose laterally and some specimens with granulate microsculpture at base, but most of tergum smooth; apical margin markedly sinuate. T3 smooth or slightly sculptured at extreme base; apex slightly desclerotized, not whitened. T4 to T7 slightly desclerotized, not whitened; setae scattered evenly across terga, but concentrated near apex of T4 in some specimens. Islands elongate oval, lengthened posteriorly. Hypopygium (fig. 118) with setae absent midventrally over most of length; apex entire medioventrally; posterodorsal margin sinuate and with a lobe. T9 approximately 3.4 times higher than wide (fig. 116). Second valvifer (fig. 116) projected well into upper 0.5 of T9, apex knobbed and with irregular or round margin. Third valvula (fig. 116) decurved, with ventral margin sclerotized and concave over most of length; setae on apical 0.75 or more, markedly concentrated near ventral side of valvula; apex with triangular and acute desclerotized area. Ovipositor (fig. 116) decurved over most of length, but markedly more so apically than basally; approximately 2.0 times as long as hind tibia, without subapical constriction; basal bulb abruptly set off from shaft.

Male. Similar to female, except: some specimens darker than female, with anteriormost laterotergites of metasoma rufofulvous; face with median carina faint, less than 0.33 of face height in some specimens; pronotum of some specimens with some rugosity in area of junction between dorsal and ventral grooves; mesoscutum with punctures slightly developed on posterior part in some specimens; propodeum with low lateroapical rugosity in some specimens; hind coxa with band of distinct punctation broadened ventrally; T1 of metasoma with very little sculpture and with sides evenly narrowed apically in some specimens; T2 with faint sculpture in some specimens; paramere obliquely truncate, moderately wide anteroventrally, markedly wider at apex than at base, length at least 0.33 of metasoma (fig. 121); aedeagus triangular in cross section throughout length and distinctly knobbed at apex(fig. 121); digitus elongate (fig. 121); basal ring evenly sclerotized, with convergent pair of robust median carinae (fig. 120).

Cocoon. Mass shape not known, but all cocoons with flattened and slightly translucent sides indicating close appression to other cocoons. One paratype from Santa Fe, New Mexico with two tightly bound cocoons pinned under adult specimen, both with flat and slightly translucent sides which indicates removal of other cocoons.

Larva (fig. 119). Gregarious. Hypostoma with two mandibular processes and marked hypostomal spur; mandible blade curved at apex, with irregular row of irregularly pointed teeth on apical 0.66; silk press apparently with thick integument, external and some internal details visible; labial sclerite approximately wide as high.

Hosts.— *S. neomexicanus* has been reared from undetermined Noctuidae (W.R.M. Mason, pers. comm.) and from *Protagrotis obscura* Barnes and McDunnough (R. Oetting, pers. comm.).

Phylogenetic Affinities.— *S. neomexicanus* is the sister species of *S. falcatus*.

Distribution.— Transcontinental in Nearctic Region, but apparently absent from southeastern U.S.A. (fig. 140) I have examined specimens from the following territories, provinces and states: **Canada**. Alberta, British Columbia, Labrador, Manitoba, Newfoundland, North West Territories, Ontario, Prince Edward Island. **United States**. Alaska, Arizona, California, Colorado, Idaho, Michigan, Minnesota, Montana, Nevada, New Mexico, Oregon, South Dakota, Utah, Washington, Wyoming. Apparently most abundant in southwestern U.S.A. (fig. 140).

Chorological Affinities.— The range of this species apparently overlaps with all other North American species of *Sathon*, and specimens have been collected at some of the same localities as those of *S. circumflexus* and *S. masoni*. *S. neomexicanus* is apparently allopatric with its sister species, *S. falcatus*.

Sathon falcatus (Nees von Esenbeck) 1834.

(Figs. 122 - 136).

Microgaster falcatus Nees von Esenbeck 1834: 175; type lost, Neotype designated by Wilkinson 1945: 133.
Microgaster equestris Haliday 1834: 242. Synonymy by Curtis 1837:116.
Apanteles equestris; Hincks 1944: 20.
Apanteles priapus Gautier & Cleu 1927: 85. Synonymy by Wilkinson 1945: 133.

Sathon falcatus; Mason 1981: 78. Neotype: female, Reinhard Collection, Berlin. No. 26943. Designated by Wilkinson (1945: 133).

Apanteles falcatus var. *minor* Fahringer 1938 = undetermined species of *ater*-group *sensu* Nixon 1965 and *Apanteles sp. sensu* Mason 1981)

Diagnosis.— **Female.** *Color.* Head and mesosoma black; metasoma black except for fulvous area on anteriormost laterotergites, but with rufofulvous band on apex of T3 in some specimens; legs rufofulvous, darkened apically to rufopiceous on tarsomeres, coxae piceous to black, but some specimens fulvous at extreme apex; third valvula dark rufopiceous to black.

Head. Occiput broadly and somewhat deeply indented medially, head arcuate in dorsal aspect (fig. 134). Oral plate narrow ventrally, with mediolateral pigment lines, dorsal margin slightly convex (fig. 131).

Mesosoma. Pronotum (fig. 122) with dorsal groove straight and slightly sculptured; ventral groove narrow, with slight foveolae, but some specimens with distinct foveolae anteriorly. Mesoscutum with punctures distinct over most of surface; almost all setae posteriorly directed. Prescutellar furrow moderately to markedly arcuate (fig. 123). Scutellum with lunule wide and with markedly curved or sinuate posterior margin (fig. 124). Propodeum (fig. 126) punctate basally, smooth apically or with low rugosity, especially near median carina; median carina line of rugosity near medioapical boss or extended over most of propodeal length; medioapical boss thickened medially.

Hind coxa with punctures deep, although slightly obscured on lateral surface in some specimens (fig. 128).

Fore wing with 1Rs+M sinuate.

Metasoma. T1 (fig. 127) smooth mediobasally and in some specimens medioapically, rugose or rugosopunctate elsewhere; apex narrower than base, with sides convergent throughout length but more so on apical 0.33 than basal 0.66, some specimens nearly as wide at apical 0.66 as at base. T2 (fig. 127) with lateral margins straight or slightly convex; rugose, but with sculpture absent medially; apical margin markedly sinuate. Hypopygium (fig. 132) with apex immarginate and posterodorsal margin angulate and somewhat sinuate. T9 approximately 3.0 times higher than wide (fig. 130). Second valvifer (fig. 130) projected well into upper 0.5 of T9, apex rounded and with distinct head set off from remainder of valvifer. Third valvula (fig. 130) more decurved apically than basally, with ventral margin concave over most of length; apex with desclerotized area small, triangular and emarginate at tip. Ovipositor (fig. 130) decurved over most of length, but markedly more apically than basally; nearly 2.0 times as long as hind tibia, with no or slight subapical constriction; basal bulb markedly set off from shaft.

Male. Similar to female, except: trochanters infuscate, apex of hind tibia, and in some specimens all femora and apex of middle tibia, extensively infuscate; scutellum with lunule wide, but not with markedly curved or sinuate posterior margin; propodeum with some lateroapical rugosity and medioapical boss triangular in some specimens; T1 of metasoma (fig. 129) evenly narrowed apically in some specimens; paramere slightly obliquely truncate, wide anteroventrally, markedly wider at apex than at base, length at least 0.33 of metasoma (fig. 136); aedeagus with sclerotized bar in dorsal surface (fig. 135), triangular in cross section throughout length, distinctly knobbed at apex (fig. 136); digitus elongate (fig. 136); basal ring evenly sclerotized, with divergent pair of robust median carinae at base (fig 135).

Cocoon. Vertically arranged in tightly bound oblong mass, some cocoons on mass periphery angled relative to central cocoons; individual cocoons with flattened and slightly translucent surfaces at areas of contact with other cocoons.

Larva. (fig. 133) Hypostoma with three mandibular processes and distinct hypostomal spur; mandible blade straight at apex, with single row of straight, regular teeth on apical 0.66; silk press apparently with thick integument, external and some internal details visible; integument dorsad each hypostoma thickened, with two faintly sclerotized bars directed posteriorly from mid-length of each hypostomal sclerite.

Hosts.— *S. falcatus* has been reared from larvae of the following species of Lepidoptera: *Noctua sp.*, *Xylophasia monoglypha* Hufn., *Eupithecia succenturiata* (L.), *Pterophorus osteodactylus* Zell., *Rhyacionia buoliana* Schiff., *Agroperina lateritia* Hufn., *Synanthedon tipuliformis* Cl. and *Hepialis humuli* L. (see Shenefelt 1972 for citations of rearing records).

Phylogenetic Affinities.— *S. falcatus* is the sister species to *S. neomexicanus* .

Distribution.— Transcontinental in the Palaearctic Region, also in Java. Published records give a range from Egypt to Sweden and from Spain to Sakhalin.

Chorological Affinities.— The range of this species overlaps with both other Palaearctic species of *Sathon*, but *S. falcatus* is the only representative of the *S. falcatus*-group in the Old World. Both *S. eugeni* and *S. lateralis* have been taken at localities where *S. falcatus* has been found. Apparently allopatric with its sister species, *S. neomexicanus*.

TAXA EXCLUDED FROM *SATHON*

Sathon falcatus var. ***minor*** **Fahringer 1938**

The specimen from which this variety was described has an areolate propodeum, aciculate mesonotal punctures, a desclerotized and striate hypopygium and sparsely setose vannal lobe of the hind wing. It keys to *Apanteles ater* - group in Nixon (1965) and *Apanteles sp.* in Mason (1981).

Lathrapanteles papaipemae Muesebeck 1921 (1920)

This species was included in *Sathon* by Mason (1981) in his original description of the genus, but was removed by Williams (1985: 1963).

PHYLOGENETIC RECONSTRUCTION

Methods

The 53 characters of table 1 were subjected to phylogenetic analysis using the methods of Hennig (1966). A phylogenetic tree of *Sathon* species was reconstructed by analysis of the distribution of shared derived character states (synapotypies), from which a classification of *Sathon* species was derived. Phylogenetic systematics was used in order that the classification derived from the phylogeny would be maximally informative about the evolution of *Sathon* species (Farris 1979, Nelson 1973).

Character states were assigned plesiotypic or apotypic polarity using outgroup comparison of character state distributions (Farris 1982, Stevens 1980). Choice of outgroup species was made difficult by the inadequate understanding of the relationship between *Sathon* and *Choeras*. If these genera are sister groups, then *Choeras* species with relatively plesiotypic character states would be most similar to the last common ancestor of both genera and would be required as an outgroup. If *Choeras* is paraphyletic to *Sathon*, then species similar to *Sathon* species, with relatively apotypic character states, would be required. An intermediate solution was chosen to attempt to allow for both possibilities. Use of this kind of generalized outgroup engenders some problems, and strict polarization criteria were necessary to insure that characters were properly analysed (see below). *Choeras* species were chosen whose character states ranged from preponderantly plesiotypic to preponderantly apotypic. Six species were chosen: *Choeras tiro* Reinhard, *Choeras consimilis* Viereck, and undecribed *Choeras* sp. A, B, C and D. These six species were found to be the minimum number necessary to represent a reasonable sample of variability in *Choeras* character states, from relatively plesiotypic states (similar to what may be considered 'groundplan' states of the Microgastrinae as judged by examination of plesiotypic members of the family such as the Apantelini and more plesiotypic Microgastrini) to apotypic states similar to those found in *Sathon*. *Choeras* sp. D is in fact very similar in habitus to *S. lateralis*-group species, except for the retention of a fully developed, setose metanotum and a midventrally creased hypopygium.

Characters with more than one state in *Sathon* were examined in all six species of *Choeras*. Those which displayed little or no variability in *Choeras* species were polarized with the plesiotypic state in *Choeras* and in the *Sathon* species which shared this state. The alternate state or states found in *Sathon*, not shared with *Choeras*, were classified as apotypic. For some characters, more than one state was shared between the genera, but the character was still used to infer phylogeny. Here, states unique to *Sathon* species were classified as apotypic, whereas all states shared between the two genera were considered plesiotypic, since no single state could be chosen on the basis of the outgroup. Since the plesiotypic state is indicated by the letter **a** in table 1, multiple plesiotypic states are indicated by the use of primes, most commonly **a'**. Similarly, apotypic states that are considered to be independently derived in unrelated species may be designated **b** or **b'**, **c** or **c'**, *et cetera*.

Characters and States

Table 1 contains all characters with distinguishable synapotypic or autapotypic states, polarized by the methods above and used to reconstruct phylogeny (fig. 137). All characters discussed in this section were used in phylogenetic reconstruction, although some were subject to difficulties in interpretation (see below). Character states are coded alphabetically. Both binary (coded **a** and **b**) and multistate (coded **a** up to **e**) characters are present. For multistate characters that form transformation series, states are coded in alphabetical order, with states increasingly apotypic. These characters are coded to indicate morphological similarity, which does not always correspond to phylogenetic relatedness, due to homoplasy. Such instances are discussed below (see 'Homoplasy'). Also, some multistate characters are difficult to interpret, so that none or not all of the states can be arranged in a morphological transformation series. These states are treated as partly or wholly unordered and coded arbitrarily. An example of this is character 10 (see below). The most plesiotypic state, **10a**, is a state of maximum puncture distinctiveness on the hind coxa. Apotypic states **10b** and **10c** form a transformation series with a trend to reduction of puncture distinctiveness. However, state **10d** includes reduction of both distinctiveness and spatial distribution on the coxa. Since **10d** could have been developed from at least two of the other states and perhaps all three, its coding as **d** is arbitrary, rather than indicating continuance of the series. Each character that presents such coding difficulties is discussed individually below. There are also characters which exhibit loss or reduction states that may be part of a transformation series where a morphologically intermediate state is interpreted as plesiomorphic. Such states are coded **-b** (e.g. character 2). Characters are numbered in the order that they appear on the cladogram, for increased correspondence between table 1 and fig. 137. Species are arranged in table 1 as in fig. 137, with those possesing a balance of plesiotypic states on the left and apotypic states on the right following phylogenetic order.

For most characters, especially autapotypies, polarization was straightforward. Here, all six species of the outgroup had the same state, and the distribution of states within *Sathon* was completely congruent with the reconstructed phylogeny. The discussion of these characters is minimal, since most of the pertinent information is given in table 1. Characters needing no further discussion are numbers 3, 7, 8, 13, 14, 15, 16, 17, 18, 19, 20, 21, 23, 24, 29, 31, 32, 33, 35, 36, 40, 41, 45, 48, 49, 51 and 53. Some characters with missing data points must be used with caution, but their known state distributions are otherwise congruent with the reconstructed phylogeny and their polarization relatively straightforward. These characters are numbers 1, 25, 26, 27, 30, 39, 42, 43 and 47. Characters 6 and 9, also with missing data points, require further discussion because of other problems in interpretation.

Characters that are more difficult to interpret require some discussion, including information on variability of the outgroup, polarization method and points of congruency or incongruency with the phylogeny. These characters are listed here. In the following discussion some species names are joined with a '+'. These species are considered to represent members of a monophyletic lineage.

Character 2. Hypopygium, setation. Three character states: plesiotypic– moderately setose (fig. 91)(**2a**); apotypic (two states)– setose area small (fig. 118)(**2-b**), and setose area large (fig. 18)(**2b**). Difficulty in interpretation of this character is in the variability of hypopygium structure in *Choeras*. The desclerotized, striate portion of the hypopygium is asetose in outgroup species. Thus, distribution and density of setae is dependent on the size of this area in *Choeras*, but not in *Sathon*. In two outgroup species, *Choeras* sp. C and D, this desclerotized area is limited to a midventral crease, and the distribution of hypopygial setation is comparable to *Sathon*. Independent increase (**2b**) and decrease (**2-b**) are hypothesized from a moderately setose hypopygium. there is apparent homoplasy between *S. laevidorsum* and the *S. lateralis*-group in state **2b**.

Character 4. T2 of the metasoma, lateral groove shape. Three character states: plesiotypic– nearly straight (fig. 127) (**4a**); apotypic (two states)– curved at base, with T2 goblet-shaped (fig. 13) (**4b**), and obscured by rugosity (fig. 73) (**4b'**). This character was difficult to polarize because only one outgroup species, *Choeras* sp. D, has a subtriangular T2 of the metasoma similar to that found in *Sathon*. This species has nearly straight lateral grooves. It is interpreted here that states **4b** and **4b'** are derived independantly from state **4a**.

Character 5. Sculpture of the lateral pits of the metanotum. Two character states: plesiotypic– completely sculptured (fig. 12) (**5a**); apotypic -partially smooth (fig. 126) (**5b**). Difference in structure of the metanotum between *Choeras* and *Sathon* causes some difficulty in polarizing this character. The metanotum of *Choeras* species is complete, with a much larger and more variably sculptured pit in the outgroup. However, the lateral pits in *Choeras* species have a groove along the posterior margin which is apparently homologus with the lateral pit of *Sathon* species. This groove is completely sculptured in the outgroup, and this is considered the plesiotypic state.

Character 6. Paramere, apex shape. Two character states: plesiotypic– rounded (fig. 22) (**6a**); apotypic– truncate (figs. 66, 121) (**6b**). The paramere of all outgroup males examined is rounded apically, except in *Choeras tiro*, where it is slightly truncate. The paramere of this species appears similar to that of *S. aggeris* (fig. 66), but is less developed. A rounded paramere apex occurs in nearly all other species of Microgastrinae exclusive of *Sathon*, and this is considered to be the plesiotypic state in *Sathon*. The truncate paramere occurring in *Choeras tiro* is considered to be an independent development.

Character 9. Second valvifer, apex shape. Five character states: plesiotypic– straight and slightly narrowed (fig. 16) (**9a**); apotypic (four states)– apically narrowed (figs. 76, 89) (**9b**), apically expanded (fig. 102) (**9c**), with sutures delimiting an apical area (fig. 130) (**9d**) and curved and anteriorly deflected (figs. 31, 34) (**9e**) (all species of *Choeras* display **9a**). The states of this character were coded arbitrarily. No transformation series were discriminated, although there may be one that has not been detected. Letter codes, rather than primes or negatives, were used only because of the high number of states found. The direction of evolution of this character is not well understood. Although there may be unresolved homoplasy, it is here interpreted that states **9b** and **9e** are synapotypies for those species that possess them.

Character 10. Hind coxa, punctation. Four character states: plesiotypic– distinct, evenly scattered (fig. 14) (**10a**); apotypic (three states)– obscure (fig. 128) (**10b**), very indistinct or absent (fig. 44) (**10c**) and limited to a midlateral band (fig. 114) (**10d**). States **10a** to **10c** form a morphological transformation series that is incongruent with the reconstructed phylogeny, while state **10d** could have been derived from any other state. It is interpreted here that state **10c** is independently derived from state **10a**, and that state **10b** in *S. falcatus* is a reversal from state **10d** found in its' most closely related species (right half of table 1).

Character 11. Metasoma color. Two character states: plesiotypic– dark, from rufopiceous to black with a white to rufofulvous anterolateral spot (**11a**); apotypic– almost entirely fulvous, except for variably developed rufopiceous to piceous areas on the base and apex of the metasoma (**11b**). The apotypic state is apparently independently derived in all three species that display it. *S. neomexicanus* is polytypic for this character, with a range of states from plesiotypic to apotypic, with intermediates.

Character 12. Propodeum sculpture. Four character states: plesiotypic– moderately developed fine wrinkles (fig. 12) (**12a**); apotypic (three states)– laterapically rugose and carinate (fig. 72) (**12b**), markedly areolate-rugose over whole surface (fig. 55) (**12b'**), and nearly smooth (figs. 27, 49) (**12-b**). Although a morphological transformation series can be seen in states **12-b**, **12a** and **12b**, this character is treated as unordered, with **12a** giving rise to both states independently. State **12b'** could have developed from any of the other states.

Character 22. Metanotal midpit, shape. Three character states: plesiotypic– sides irregular or curved, in some specimens slightly anteriorly divergent (fig. 27) (**22a**); apotypic (two states)– sides anteriorly convergent (fig. 49) (**22b**), and sides anteriorly divergent (fig. 112) (**22-b**). Although an apparent transformation series exists in states **22-b**, **22a** and **22b**, it is interpreted here that states **22-b** and **22b** are independantly derived from state **22a**. However, the outgroup state is somewhat variable, with sides curved or irregular and not exactly like state **22a** in some outgroup species.

Character 28. Third valvula, shape. Three character states: plesiotypic– straight (fig. 16) (**28a**), or slightly decurved (fig. 53) (**28a'**); apotypic– markedly decurved (fig. 130) (**28b**). States **28a** and **28a'** are found in both genera as two discrete states. It is not possible to confidently assign an apotypic polarity to either state because of this distribution, although one state is presumably apotypic. This character is useful, despite coding of two states as possibly plesiotypic, since state **28b** remains a useful synapotypy for those *Sathon* species that display it. Further study may give greater resolution of the evolution of this character.

Character 34. Sculpture of T1 of the metasoma. Three character states: plesiotypic– moderately rugose overall, with sculpture reduced in the mediobasal groove (fig. 13) (**34a**); apotypic (two states)– entirely markedly rugose (figs. 56, 86) (**34b**), and reduced to lateroapical punctures (fig. 50) (**34-b**). Independent increase (**34b**) and decrease (**34-b**) in sculpture are apparently derived from the moderately rugose state (**34a**). Differences between species in type of sculpture in state **34b** indicate independent origin twice.

Character 38. Ovipositor, decurvature. Four character states: plesiotypic– slightly and evenly decurved over most of length (fig. 16) (**38a**); apotypic (three states)– markedly and evenly decurved over most of length (fig. 102) (**38b**), markedly decurved at apex, slightly decurved elsewhere (fig. 116) (**38b'**), and with a sharp subapical bend, slightly decurved or straight apicad and distad of bend (fig. 89) (**38b"**). Two states appear in the outgroup, **38a** and a state similar to **38b'** but markedly less developed. Since the latter state does not appear in *Sathon*, the former state, **38a** is classified as plesiotypic. The high degree of distinctiveness among states prevents resolution of possible transformation series. All three apotypic states are provisionally accepted as being derived independently.

Character 44. Ovipositor length/ hind tibia length. Three character states: plesiotypic– ratio approximately 1.0 (**44a**); apotypic (two states)– ratio approximately 1.5 (**44b**), and approximately 2.0 (**44c**). The plesiotypic state appears interspecifically variable, ranging from approximately 0.75 to 1.25 in both genera. Several possibly discrete states may be subsumed under the plesiotypic coding, but outgroup variability prevents discrimination of other apotypic states.

Character 46. Third valvula length/ hind tibia length. Two character states: plesiotypic– ratio approximately 0.75 (**46a**); apotypic– ratio approximately 1.0 (**46b**). The plesiotypic state appears interspecifically variable, ranging from approximately 0.60 to 0.85 in both genera. As for character 44, recognition of several possible apotypic states is prevented by high variability in the outgroup.

Character 50. Occiput of head, indentation. Three character states: plesiotypic– narrowly and shallowly indented (fig. 1) (**50a**); apotypic (two states)– broadly and shallowly indented (fig. 105) (**50b**), and broadly and deeply indented, head appearing arc-shaped in dorsal aspect (fig. 134) (**50c**). These states form an apparent transformation series that is incongruent with the reconstructed phylogeny, unless state **50a** in *S. neomexicanus* is a reversal.

Character 52. Hypopygium apex, shape. Two character states: plesiotypic– apex entire and pointed (fig. 118) (**52a**); apotypic– apex immarginate, flattened in lateral aspect (fig. 132) (**52b**). Both states appear in the outgroup. Emargination of the apex, however, is found in *Choeras* species with a large desclerotized and striate midventral area. *Choeras* species with this area reduced, and the hypopygium more comparable to that of *Sathon* species, display state **50a**.

Table 1. Characters used in Phylogenetic Analysis.

For discussion of characters see text. lat = *S. lateralis*, pap = *S. papilionae*, eug = *S. eugeni*, lev = *S. laevidorsum*, agg = *S. aggeris*, mas = *S. masoni*, cin = *S. cinctiformis*, cir = *S. circumflexus*, neo = *S. neomexicanus*, fal = *S. falcatus*. a or a' = plesiotypic; b or b', c, d, e = apotypic; - = unknown.

Characters	lat	pap	eug	lev	agg	mas	cin	cir	neo	fal
1. T9 anterior margin	b	b	b	–	–	a	a	a	a	a
a = curved										
b = deeply indented										
2. Hypopygium setae	b	b	b	b	a	a	a	-b	-b	-b
a = sparse										
b = dense										
-b = very sparse										
3. T6+T7 sclerotization	b	b	b	a	a	a	a	a	a	a
a = sclerotized										
b = desclerotized										
4. T2 groove shape	b	b	b	a	a	b'	b'	a	a	a
a = straight										
b = curved										
b' = obscured										
5. Metanotal lateral pit sculpture	a	a	a	b	b	b	b	b	b	b
a = complete										
b = incomplete										
6. Paramere apex shape	a	–	–	–	b	b	b	b	b	b
a = round										
b = truncate										
7. Third valvula sculpture	a	a	a	b	b	b	b	b	b	b
a = matte, striate										
b = polished, smooth										
8. Hypopygium margin shape	a	a	a	b	b	c	c	b	b	b
a = curved										
b = sinuate										
c = angulate										
9. Second valvifer apex shape	a	e	e	–	–	b	b	c	a	d
a = straight										
b = apically narrowed										
c = apically expanded										
d = with sutures										

(continued on next page)

Table 1 (continued)

Characters	lat	pap	eug	lev	agg	mas	cin	cir	neo	fal
e = curved										
10. Hind coxa punctation	a	a	c	a	a	d	d	d	d	b
a = marked										
b = obscure										
c = absent										
d = in midlateral band										
11. Metasoma color	a	a	b	a	a	a	b	a	a-b	a
a = rufopiceous										
b = fulvous										
12. Propodeum sculpture	a	-b	a	-b	b'	b	b	a	a	a
a = wrinkled										
b = lateroapically rugose										
b' = areolate rugose										
-b = smooth										
13. Tarsal claw shape	a	a	a	b	b	a	a	a	a	a
a = stout										
b = elongate										
14. SC+R bulb	a	a	a	b	b	a	a	a	a	a
a = absent										
b = present										
15. Cu+cu-a curvature	a	a	a	b	b	a	a	a	a	a
a = flat or curved										
b = sinuate										
16. Third valvula apex band	a	a	a	b	a	a	a	a	a	a
a = absent										
b = present										
17. Sexual dimorphism	a	a	a	a	b	a	a	a	a	a
a = moderate										
b = marked										
18. T1 convexity	a	a	a	a	b	a	a	a	a	a
a = slight or moderate										
b = marked										
19. Metanotum rim	a	a	a	a	b	a	a	a	a	a
a = absent or partial										
b = complete, foveolate										

(continued on next page)

Table 1 (continued)

Characters	lat	pap	eug	lev	agg	mas	cin	cir	neo	fal
20. Metapleural posterior carina	a	a	a	a	b	a	a	a	a	a
a = narrow, round										
b = widened, angulate										
21. Propleuron sculpture	a	a	a	a	b	a	a	a	a	a
a = punctate										
b = striate										
22. Metanotal midpit sides	a	a	a	b	b	-b	-b	-b	-b	-b
a = curved										
b = anteriorly convergent										
-b = posteriorly convergent										
23. Metanotal posterior margin	a	a	a	a	a	b	b	b	b	b
a = convex										
b = concave										
24. Midtibial inner spur length	a	a	a	a	a	b	b	b	b	b
a = long										
b = short										
25. Paramere apex width	a	–	–	–	a	b	b	c	c	c
a = narrowed										
b = slightly widened										
c = wide										
26. Digitus length	a	–	–	–	a	b	b	c	c	c
a = short										
b = elongated										
c = long, finger-like										
27. Aedeagus shape	a	–	–	–	a	b	b	b	b	b
a = oval cross-section, apex rounded										
b = triangular cross-section, apex knobbed										
28. Third valvula shape	a	a	a	a'	a	b	b	b	b	b
a = straight										
a' = apically decurved										
b = decurved										
29. Ovipositor base shape	a	a	a	a	a	b	b	b	b	b
a = gradually widened										
b = abruptly widened										

(continued on next page)

Table 1 (continued)

Characters	lat	pap	eug	lev	agg	mas	cin	cir	neo	fal
30. Second valvifer length	a	a	a	–	–	b	b	a	a	a
a = long										
b = short										
31. Ovipositor constriction	a	a	a	a	a	b	a	a	a	a
a = none or moderate										
b = marked										
32. Propodeal spiracle placement	a	a	a	a	a	b	a	a	a	a
a = close to pleural carina										
b = far from pleural carina										
33. Antennal scape color	a	a	a	a	a	a	b	a	a	a
a = concolorous with flagellum										
b = fulvous										
34. T1 sculpture	a	a	a	-b	b	a	b	a	a	a
a = moderately rugose										
b = markedly rugose										
-b = smooth										
35. Third valvula color	a	a	a	a	a	a	b	a	a	a
a = rufopiceous to black										
b = fulvous										
36. Third valvula seta shape	a	a	a	a	a	a	b	a	a	a
a = straight										
b = bent-tipped										
37. Metapleural sculpture	a	a	a	a	a	a	b	a	b'	a
a = slightly punctate										
b = rugose										
b' = markedly punctate										
38. Ovipositor decurvature	a	a	a	a	a	a	b"	b	b'	b'
a = even, slight										
b = even, marked										
b' = apically decurved										
b" = sharp subapical bend										
39. Basal ring sclerotization	a	–	–	–	a	a	a	b	b	b
a = medially desclerotized										
b = evenly sclerotized										

(continued on next page)

Table 1 (continued)

Characters	lat	pap	eug	lev	agg	mas	cin	cir	neo	fal
40. Oral plate color	a	a	a	a	a	a	a	b	b	b
a = unicolorous										
b = medially pigmented										
41. T2 posterior margin shape	a	a	a	a	a	a	a	b	b	b
a = curved										
b = bisinuate										
42. Paramere length	a	–	–	–	a	a	a	b	c	c
a = short										
b = elongated										
c = long										
43. Basal ring carinae	a	–	–	–	a	a	a	b	c	c
a = absent										
b = one, slender										
c = two, robust										
44. Ovipositor length/ hind tibia length	a	a	a	a	a	a	a	b	c	c
a = approx. 1.0										
b = approx. 1.5										
c = approx. 2.0										
45. T2 of male length	a	a	a	a	a	a	a	b	a	a
a = length = width										
b = length more than width										
46. Third valvula length/ hind tibia length	a	a	a	a	a	a	a	a	b	b
a = 0.75 or less										
b = 1.0 or more										
47. T9 height/ length	a	a	a	–	–	a	a	a	c	b
a = 2.0 - 2.5										
b = 3.0										
c = 3.5										
48. Paramere truncation shape	a	a	a	a	a	a	a	a	b	a
a = ventrally oblique										
b = dorsally oblique										
49. 3Rs apex curvature	a	a	a	a	a	a	a	a	b	a
a = straight or curved										
b = decurved										

(continued on next page)

Table 1 (continued)

Characters	lat	pap	eug	lev	agg	mas	cin	cir	neo	fal
50. Occiput indentation a = narrow, shallow b = wide, shallow c = wide, deep	a	a	a	a	a	a	a	b	a	c
51. Oral plate shape a = wide ventrally b = narrowed ventrally	a	a	a	a	a	a	a	a	a	b
52. Hypopygium apex shape a = entire b = emarginate	a	a	a	a	a	a	a	a	a	b
53. Paramere base shape a = narrow b = wide	a	a	a	a	a	a	a	a	a	b

Reconstructed Phylogeny

The reconstructed phylogeny of *Sathon* species is diagrammed in fig. 137. Species that have more plesiotypic character states are placed toward the left side of the cladogram, while those with more apotypic states are placed toward the right, within the constraints of the branching pattern. Hence, the *S. lateralis*-group as a whole is considered more plesiotypic overall than the *S. falcatus*-group, while *S. neomexicanus* and *S. falcatus* are considered to be the most apotypic overall of all *Sathon* species. This is also reflected in the placement of species in sister species pairs, with the species to the right having more apotypic states. All apotypic states of a species not shared with the sister species or group are listed beside the branch representing that species.

Each dichotomy is supported by at least one apotypic character state. Apotypic states that support each dichotomy are listed beside the black square used to indicate apotypic states. Character numbers are as listed in table 1, along with the letter code for the state of that character which occurs at that branch. Dichotomies are given letter codes in upper case whose order approximately corresponds to the phylogenetic sequence. Generally, a greater number of apotypic states occurs in dichotomies to the right of the cladogram. This is due in part to the overall apotypy of the *S. falcatus*-group relative to the *S. lateralis*-group. Also, there is accumulation of multistate characters that have their most apotypic states in *S. neomexicanus* and *S. falcatus* and form transformation series that are important indicators of phylogeny. This is shown by the appearance toward the right of characters whose numbers have appeared in more basal dichotomies.

Synapotypic character states.— Many character states are shared among *Sathon* species and apparently contain information about their relationships. In the following discussion these characters are examined as they appear in the dichotomies, beginning with the most basal (A) and ending with the most apical (E). As the character states supporting either side of a dichotomy are discussed they are ranked according to degree of 'reliability' or 'confidence' they give to the monophyletic unit they define. This ranking refers only to a within-group comparison of each set of states and represents an approximate weighting system with the following criteria. Generally, any character, binary or multistate, that displays no homoplasy, has been examined in all *Sathon* and outgroup species and has been confidently polarized within the limits of the polarization method (see 'Phylogenetic Reconstruction. Methods') is considered the most reliable type. Characters which fail to meet these criteria are considered less reliable in proportion to the number of criteria they violate. For example, state **3b** is interpreted as a synapotypy which defines the *S. lateralis*-group in dichotomy A. This **b** state has been examined in all *Sathon* and outgroup species and is apparently unique to the *S. lateralis*-group. In contrast, state **1b** is considered less reliable because the state in *S. laevidorsum* and *S. aggeris* is unknown. If these two members of another species group (as suggested by the weight of evidence) were possessed of state **1b** then the use of this state as a synapotypy for the *S. lateralis*-group is weakened. Similarly, multistate characters whose transformation series have been analysed are considered more reliable than those whose states have been left partially or wholly unordered. In the following section, each set of characters supporting a monophyletic unit is discussed, followed by a discussion of autapotypies. To understand how the characters were ranked, frequent reference to table 1 and fig. 137 is recomended.

Of the synapotypies for the *S. lateralis*-group (left side of dichotomy A), middorsal desclerotization of T6+T7 of the metasoma (character 3) is considered the most reliable. There are no missing data points and only one apotypic state. The middorsal desclerotization is either marked **3b** or very slight **3a**. For character 1, female genitalia are not completely known for all *Sathon* species, so there are missing data points. Hypopygial setation (character 2) is difficult to polarize (see above), and also displays homoplasy in the development of a densely setose hypopygium in *S. lateralis*-group species and *S. laevidorsum*. The obscured lateral grooves of the metasoma (character 4) of *S. masoni* + *S. cinctiformis* could have been derived from the state found in *S. lateralis*-group species. The pattern of evolution of this character is uncertain and its value as a synapotypy for the *S.*

lateralis-group is reduced.

Both characters 5 and 7 are considered reliable synapotypies for the *S. falcatus*-group (right side of dichotomy A). Lateral pit sculpture (character 5) varies in the *S. falcatus*-group, and it is difficult to polarize states (see above), but states are distinct and there is no apparent homoplasy. Interpretation of third valvula sculpture (character 7) is straightforward. As Mason (1981) has noted, the apotypic state of third valvula sculpture is distinctive among members of the tribe Microgastrini for those *Sathon* species that display it. For character 6, paramere apex shape, there are missing data points and some difficulty in polarization (see above). For character 8 there is a transformation series, but angulate hypopygium of *S. masoni* + *S. cinctiformis* could have been derived from the plesiotypic state of the *S. lateralis*-group. This reduces the value of the specialized hypopygium as a synapotypy for the *S. falcatus*-group.

Only one apotypy is given for dichotomy B. The three species of the *S. lateralis*-group are very similar to one another, with *S. papilionae* and *S. eugeni* having few apotypic states, and *S. lateralis* apparently with none. *S. papilionae* + *S. eugeni* share one of the few apotypic states in *S. lateralis*-group species. Character 9, shape of the second valvifer apex, displays considerable variability. There may be unresolved transformation series and there are missing data points in those species where females were not dissected. Although this character is of the female genitalia, which seem to be important in the evolution of *Sathon* species (see 'Evolutionary Trends'), the phylogenetic arrangement of the *S. lateralis*-group should be considered tentative.

Of the characters supporting the left side of dichotomy C, characters 13 and 14 are considered the most reliable. Both the elongate tarsal claws and hind wing SC+R bulb are distinctive states that are unique to *S. laevidorsum* + *S. aggeris* among all *Sathon* and outgroup species examined. Character state **15b**, Cu+cu-a sinuation, is also apparently uniquely derived, but the plesiotypic state of this vein is variable in degree of curvature. Shape of the metanotal midpit (character 22) displays a posible transformation series, but has some difficulties in polarization due to variability of the outgroup.

Numerous characters support the right side of dichotomy C, of which character 29 is considered the most reliable. Slightly versus markedly widened ovipositor bases are distinct, and the markedly widened base is apparently uniquely derived. Character 10 is highly varied, displaying homoplasy in reduction of hind coxa punctures in *S. eugeni* and *S. falcatus*. If the limitation of hind coxa punctures to a midlateral band is assumed to be synapotypic for species on the right side of dichotomy C, then the uniformly but slightly punctate hind coxa of *S. falcatus* must be a reversal. As mentioned above, character 22, shape of the metanotal midpit, is difficult to interpret. Characters 25 to 27 are of the male genitalia, and display missing data points. Although these characters are considered important in later dichotomies (see below), one of the species resolved by dichotomy C is missing this information. The shape of the posterior margin of the metanotum (character 23) is varied in species with the apotypic state, implying that the concave margin is labile and perhaps not uniquely derived. Character 24, length of the midtibial inner spur, is considered moderately reliable, but does display some variability of spur length in the plesiotypic state. Variability of the outgroup for character 28, third valvula shape, necessitates classification of two states as plesiotypic. This variability reduces the value of the apotypic state as a synapotypy, and incomplete resolution of state polarities may obscure homoplasy.

All of the characters on the left side of dichotomy D display some problems in interpretation. Characters 4 and 8 are considered the most reliable, although they share a similar problem in interpretation. Both the obscured lateral grooves of T2 and the angulate posterodorsal margin of the hypopygium could have been derived from either alternate state for each character. While this does not markedly affect the value of these states as synapotypies for *S. masoni* + *S. cinctiformis*, it does affect their placement relative to other species pairs. For character 9, second valvifer apex shape, the pattern of evolution of states is unclear, and although the reduced state found in *S. masoni* + *S. cinctiformis* is unlikely to be ancestral to any other state seen in *Sathon*, uncertainty is caused by the obvious lability this character displays. Character 12, propodeal sculpture, has been discussed above. The similarity of lateroapically sculptured states in *S. masoni* and *S. cinctiformis* indicates that this is a synapotypy for these species, but there is a similarity at least in trend in *S. aggeris*. Length of the second valvifer (character 30) in unknown in two *S. falcatus*-group species, and is probably functionally correlated with the narrowed and reduced apex shape found in *S. masoni* + *S. cinctiformis* (character 9).

The right side of dichotomy D is supported by nine synapotypies. The most reliable of these are binary characters 40 and 41, and multistate character 44. Also given considerable weight are multistate characters 25, 26, 42 and 43, although there are missing data points for these characters. They are considered important because they display transformation series, whose clear set of states in character evolution give increased information on phylogeny. Although such characters appear in dichotomy C, these characters offer the most resolution in dichotomies D and E. Characters 40 and 41, oral plate color and T2 posterior margin shape, are of unique derivation and are very distinctive. The oral plate is either unicolorous or has distinct pigment lines. The posterior margin of T2 may be variably curved in the plesiotypic state, but is nearly straight, whereas the apotypic state is markedly bisinuate. Ovipositor length (character 44) is variable in the plesiotypic state, but displays a clear apotypic increase in *S. circumflexus* + *S. neomexicanus* + *S. falcatus*. Characters 25, 26, 42 and 43 are male genital characters which display obvious transformation series in spite of missing data points (table 1). Character 2, hypopygial setation, displays an apotypic reduction of setae in *S. circumflexus* + *S. neomexicanus* + *S. falcatus*, but interpretation of polarity of this character is uncertain (see above). Character 39 has missing data points and does not display a transformation series. There is some variability in degree of sclerotization of the basal ring in both states, and the more sclerotized state may be functionally correlated to character 43, presence of basal ring carinae.

The placement of *S. neomexicanus* and *S. falcatus* as sister species in dichotomy E is supported by characters of the male and female genitalia. As in dichotomy D, multistate characters with apparently clear transformation series are important, comprising four of the six characters and displaying their most apotypic states in *S. neomexicanus* + *S. falcatus*. Characters 44 and 46 are considered the most reliable. Both are characters of the female genitalia and display no missing data points. The plesiotypic states of these characters are various, but the states classified as apotypic are distinctive. Character 47 has similar attributes, but displays missing data points. Characters 42 and 43 are of the male genitalia. They display transformation series, but are given slightly less weight because of missing data points. Ovipositor shape (character 38) displays three apotypic states in the four species considered most apotypic overall. Although neither of the states in *S. cinctiformis* and *S. circumflexus* are similar to the apically decurved state found in *S. neomexicanus* + *S. falcatus*, there may be an unresolved transformation series, with the entirely decurved ovipositor in *S. circumflexus* derived from the apically decurved ovipositor. However, each of the three states is distinctive enough that they all show the same degree of divergence from the ancestral state, and there is no information on function to aid in hypothesizing an evolutionary sequence of states.

Autapotypic Character States.— There are two types of autapotypic states found in the cladogram. Some states are apparently unique to a species and derived only once. Others are apotypic states not shared by the sister species or group, but the same or similar states may be found in other *Sathon* species. States of the second group were interpreted as autaoptypies only after the phylogenetic analysis was complete. Both types have a similar function in the cladogram when differentiating between sister species and deciding position on the cladogram based on the number of apotypic states each species has. Every species on the cladogram has autapotypic states assinged except *S. lateralis*. No apotypic states were assignable to *S. lateralis* that would differentiate this species from other members of the *S. lateralis*-group. There are characters whose states are unique to *S. lateralis* within the *S. lateralis*-group (see table 3), but these could not be reliably polarized. Apotypic states in *S. lateralis* are synapotypic for the entire species group (characters 1 to 4).

S. papilionae is apotypic for character 12. The reduction of propodeal sculpture found in this species is also found in *S. laevidorsum*. This state differentiates *S. papilionae* from other *S. lateralis*-group species, but displays homoplasy.

There are two apotypic states in *S. eugeni*. In both characters, 10 and 11, there are multiple apotypic states and apparent homoplasy. In character 10, hind coxa punctation, the state in *S. eugeni* is unique in that punctures are more completely obscured than in any other *Sathon* species. A possible transformation series may be seen in the moderately obscured punctation of the hind coxa of *S. falcatus*. This may be considered intermediate between the fully punctate plesiotypic state and the state in *S. eugeni*, but the resulting transformation series is incongruent with the reconstructed phylogeny. In character 11, a predominantly fulvous metanotum is shown in *S. eugeni*, *S. cinctiformis* and some specimens of *S. neomexicanus*. Each of these occurrences is considered independently evolved.

S. laevidorsum is apotypic in three characters that are plesiotypic in its sister species, *S. aggeris*. In character 16, the sclerotized band within the desclerotized third valvula apex is found only in *S. laevidorsum*, and although this apex may vary in shape and size among *Sathon* species, it is always uniformly desclerotized in the plesiotypic state. Character 2 and 12 display homoplasy. The dense setation of the hypopyium of *S. laevidorsum* is apparently also a synapotypy for *S. lateralis*-group species. As mentioned above, both *S. papilionae* and *S. laevidorsum* have a relatively smooth propodeum. In addition, *S. laevidorsum* is apotypic in character 34, with a smooth metasomal T1, unlike its sister species which has a different apotypic state.

S. aggeris is apparently a very autapotypic species, considering its relatively basal placement in the *S. falcatus*-group on the cladogram. Four of the seven characters (nos. 17, 18, 20 and 21) listed for this species are unique derivations. Each of the states, marked sexual dimorphism, T1 bulbosity, angulate metapleural carina and striate propleuron are distinctive and markedly differentiated from relatively invariable plesiotypic states. Propodeal sculpture (character 12) in *S. aggeris* is unique within the genus, but propodeal sculpture is varied in both *Sathon* and the outgroup. The state of character 19, rim of the posterior margin of the metanotum, can also be considered autapotypic, although a transformation series may occur if the slight rim in other *Sathon* species is considered apotypic. *S. aggeris* is also apotypic for character 34, with a markedly sculptured T1 of the metasoma that is unlike the apotypic state found in its sister species *S. laevidorsum.*

S. masoni is apotypic for characters 31 and 32. Both states are apparently unique derivations in *S. masoni*, but the plesiotypic states of both subapical ovipositor constriction and propodeal spiracle placement are variable. Further resolution of these characters could yield other apotypic states and possible transformation series.

S. cinctiformis has apotypic states in seven characters not shared with the sister species, *S. masoni*, the greatest number found for one species. Unlike *S. aggeris* however, only three of seven states, in characters 33, 35 and 36, are uniquely derived. *S. cinctiformis* is one of the lightest colored *Sathon* species, as can be seen in the unique fulvous color of the antennal scape (character 33) and third valvula (character 35). *S. cinctiformis* is also one of three *Sathon* species to independently develop a fulvous metasoma (character 11). *S. cinctiformis* is unique in third valvula setae (character 36), with bent-tipped setae near the apex of the valvula. In character 34, the rugosity of T1 of the metasoma in *S. cinctiformis* displays some similarity to the state found in *S. aggeris*. Rugosity of the metapleuron (character 37) is unique to *S. cinctiformis*, but there is another apotypic state in *S. neomexicanus*. The apotypic decurvature of the ovipositor (character 38) in *S. cinctiformis* is superficially similar to that of *S. neomexicanus* + *S. falcatus*.

S. circumflexus is apotypic for four characters, 9, 38, 45 and 50, but only character 45, shape of T2 of the metasoma in males, is unique. Character 9, second valvifer apex shape, is highly variable, with uncertainty in ordering of states (see above). This is also true of ovipositor decurvature (character 38). Occiput indentation (character 50) displays an apparent transformation series, with the state in *S. circumflexus* intermediate between the plesiotypic state and that found in *S. falcatus*. However, this transformation series is incongruent with the reconstructed phylogeny unless the plesiotypic state in *S. neomexicanus* is a reversal.

S. neomexicanus is autapotypic for characters 48, paramere apex truncation shape, and 49, 3Rs apex curvature. The plesiotypic states of both characters are varied. Fulvous metasomal color (character 11) has apparently been evolved three times in *Sathon* and is polytypic in *S. neomexicanus*. The markedly punctate metapleuron (character 37) of *S. neomexicanus* is somewhat like the apotypic state found in *S. cinctiformis*, and is not considered unique. The apotypic state of character 47, T9 height/ length, represents the most apotypic state in a transformation series.

S. falcatus is autapotypic for characters 51, 52 and 53. This species alone in *Sathon* has a ventrally narrowed oral plate, an apically emarginate hypopygium and a wide band at the base of the paramere. Other apotypic states include a state of the highly variable second valvifer apex (character 9), an apparent intermediate state in hind coxa punctation (character 10) and a deeply indented occiput (character 50). The last two characters represent states in transformation series that are incongruent with the reconstructed phylogeny.

Homoplasy.— Characters that display homoplasy in *Sathon* have been noted above, under the discussion of characters and the reconstructed phylogeny. A brief summary is given here and in table 2. Homoplasy is considered to be present when the distribution of a state or states is incongruent with the reconstructed phylogeny, displaying parallelism or convergence. Incongruence is judged on the weight of evidence, since most of the characters in table 1 support the reconstructed phylogeny. Homoplasy is exhibited by characters 2, 10, 11, 12, 34, 38 and 50. In characters 2, 11 and 12 essentially identical apotypic states are in non-sister groups. In characters 10 and 50, apparent homoplasy involves dissimilar states that may be considered members of transformation series that are incongruent with the reconstructed phylogeny. Characters 34 and 38 have states in non-sister species that are similar in general and display similar direction of evolution, but are different in detail. This difference is assumed to indicate different origins of the states. For character 34 there is an increase of sculpture of T1 of the metasoma in two species. For character 38 there is decurvature of the ovipositor in three species, yielding two different states.

There is a general correlation between character lability and homoplasy. Of the characters listed above, only character 11 is binary. All others are multistate. Three of four characters with four or more states display homoplasy, character 9 the exception. In this character the direction of evolution has not been well worked out. Just as there may be an unresolved transformation series in this character, there may also be unresolved homoplasy. This is apparently a straightforward correlation between frequency or ease of character change through selection or drift and likelihood that a particular state will arise more than once.

Also, there is apparently little homoplasy in characters of the genitalia. Only two characters displaying homoplasy (2, 39) are of the genitalia, though genitalia comprise 26 of 53 characters used. This lack of homoplasy is a factor in the overall reliability of genital characters as phylogenetic indicators.

Common evolutionary pressures result in much homoplasy through convergent development of adaptations in unrelated species (Mayr 1963). In *Sathon*, too little is known about life histories to understand common factors that might cause homoplasy of any states in table 2. For example, the similarity of states **38b'** and **38b''** for ovipositor shape may be due to some host dependent factor. However, there are no hosts known for *S. circumflexus*, females of which display **38b''**, nor is it known what function apical decurvature serves in host finding or penetration. This inadequacy of understanding is true for both homoplasious and congruent characters.

Table 2 summarizes homoplasy in characters of table 1. Characters are listed by number, with states displaying homoplasy or incongruent transformation series and taxa involved.

Evolutionary Trends

Some generalizations emerge about the evolution of *Sathon* species and the characters that vary among them. Significant features of evolution are examined at the level of changes in characters and character complexes, and at the level of species evolution.

Features of Characters and Functional Complexes.— Characters of table 1 are in three main groups: female genitalia; male genitalia; and non-genital features of adult structure. Characters of the female genitalia that vary are those associated with host finding and oviposition, those of the male genitalia are associated with possible reproductive isolating mechanisms and those from the third group serve a wide variety of functions.

Female genitalia.— Characters 1, 2, 7, 8, 9, 16, 28, 29, 30, 31, 35, 36, 38, 44, 46, 47 and 52: These are of the female genitalia, including T9 of the abdomen and the hypopygium as a functional complex. These characters make up the largest single block from any one functional body part (*versus* sets of characters from the head, appendages or other such groupings). These characters appear in each dichotomy of fig. 137 and could support the entire cladogram without reference to any other

Table 2. Characters of Table 1 displaying homoplasy in *Sathon* species.

For explanation of characters see text. TS = transformation series, Freq. = number of times evolved.

Character	State	Freq. or TS	Taxa displaying homoplasy
2	b	2	*S. lateralis*-group and *S. laevidorsum*
10	b,c	TS	*S. eugeni* and *S. falcatus*
11	b	3	*S. eugeni*, *S. cinctiformis* and *S. neomexicanus*
12	-b	2	*S. papilionae* and *S. laevidorsum*
34	b	2	*S. aggeris* and *S. cinctiformis*
38	b',b"	2	*S. cinctiformis* and *S. neomexicanus* + *S. falcatus*
50	b,c	TS	*S. circumflexus* and *S. falcatus*

character system. They comprise also the largest block of multistate characters in table 1 (7 of 18). Additionally, characters of the female genitalia display little intraspecific variability, and little interspecific variability in the outgroup or in *Sathon* species that have plesiotypic character states. For these reasons, characters of the female genitalia are considered very important in the evolution of *Sathon* and in the analysis of phylogenetic relationships.

The factors involved in this divergence of female genital structures are uncertain, but host type is probably important. Mason (1981) has hypothesized that evolution of female genitalia in the Microgastrinae is related to changes in host preference. Rearing data for *Sathon* species indicate a wide range of host types, since plesiotypic species (*S. lateralis* and *S. eugeni*) are solitary parasitoids of microlepidopterans, while apotypic species (*S. neomexicanus* and *S. falcatus*) are gregarious parasitoids of macrolepidopterans. Unfortunately, no host data are known for *Sathon* species that are intermediate in structural apotypy. Information on these species might aid in understanding selective forces producing change in *Sathon* female genitalia. Length of the ovipositor, for example, is correlated with physical location of the host. Plesiotypic *Sathon* species have relatively short ovipositors and probably parasitize larvae that are exposed, or near the substrate surface (*S.*

papilionae parasitism of *Papilio zelicaon* Lucas, for example). Apotypic species have relatively long ovipositors and probably parasitize more deeply hidden hosts (*S. falcatus* parasitism of *Rhyacionia buoliana* Schiff, for example). However, there are no rearings of *Sathon* species with ovipositors of intermediate length. Also, too little is known about oviposition behavior to hypothesize how hosts effect other characters, such as shape of the ovipositor apex, shape of the second valvifer, etc.

Male genitalia.— Characters 6, 25, 26, 27, 39, 42, 43, 48 and 53: These characters appear in every dichotomy in figure 137 outside of the *S. lateralis*-group (where two of three species are not known from males). Four multistate characters are of the male genitalia, with distributions of states congruent with those of the female genitalia. Despite the absence of data about *S. papilionae*, *S. eugeni* and *S. laevidorsum*, which are not known from males, the male genital complex contains much information about *Sathon* evolution, so male genital characters are considered important in analysis of relationships. As with female genitalia, interspecific variability is high, while intraspecific variability is relatively low.

Interspecific differences in male genitalia are regarded generally as functioning in reproductive isolation (Mayr 1963). Each species of *Sathon* that is known from males has a distinctive combination of plesio- and apotypic character states that make male genitalia diagnostic. This feature may indicate that mechanical reproductive isolation may be more important in *Sathon* than in other Microgastrinae where genital divergence is low.

Other characters. Genital characters comprise nearly half (26 of 53) of characters used in the reconstructed phylogeny. The remaining 27 characters are non-genital features of adult structure. No single functional complex is dominant in this third block of characters, taken in approximately equal numbers from appendages, mesosoma and metasoma, although there are few characters from the head. Most characters in this group are more intra- and less interspecifically variable than genital characters. This would indicate a lower level of normalizing selection than on complexes that perform the important tasks of reproduction and host finding. However, some groupings in this third block of characters show enough variation that they may be significant in the life histories and evolution of *Sathon* species.

Shapes of sclerites of the anterior end of the metasoma (T1 and T2) show significant variation and are the source of many useful diagnostic characters, both in *Sathon* and in the Microgastrinae as a whole (Mason 1981, Nixon 1965). In *Sathon*, shapes and sculpture of T1 and T2 also yield characters for phylogenetic reconstruction (nos. 4, 18, 34, 41 and 45. See also unpolarized character 70, table 3). The selective forces determining states of these sclerites are not understood, but differences in states may affect mobility of the metasoma, which in turn may affect oviposition or copulatory behavior.

Sculpture is a prominent feature in the structure of *Sathon* species, in areas other than T1 and T2 of the metasoma (See characters 5, 7, 10, 12, 19, 21, 34 and 37. See also unpolarized characters of table 3, nos. 55, 62, 63 and 67). In three species sculpture shows definite tendencies, for reason unknown. *S. aggeris* and *S. cinctiformis* tend to be markedly sculptured, a convergent tendency with different end results (compare figs. 55-63 with 81-88). *S. laevidorsum*, as the name implies, tends to have reduced sculpture. The pattern of sculpture evolution is unclear, given that *S. laevidorsum* and *S. aggeris* are sister species, and that most modifications in other species appear as autapotypies or unpolarized states not shared with sister groups. Perhaps there is a component of genetic drift in sculpture changes.

Features of Taxa.— The most marked phenomenon in the evolution of *Sathon* species is the difference between the *S. lateralis*- and *S. falcatus*-groups. Species of the *S. lateralis*-group are very similar to one another in habitus and display few apotypic features. There is little character change or morphological divergence between species. This is demonstrated by the overall lack of support in shared derived characters for this section of the cladogram (fig. 137). The only synapotypic feature in this section of the cladogram is for very labile character 9, and there are no unique apotypic states in any *S. lateralis*-group species. In contrast, species of the *S. falcatus*-group have numerous apotypic states. Each species has at least one autapotypy and most species have several. Species are morphologically distinct from one another, as is shown by the relatively large number of apotypic states that differentiate each species and its sister group (fig. 137).

This can be illustrated by examining multistate characters, which display the most evolution. Only the 11 multistate characters which display no missing data points (no.s 2, 4, 8, 10, 12, 22, 28, 34, 37, 38 and 50) are examined. *S. lateralis*-group species are apotypic in only four of these characters (2, 4, 10 and 12), and character change occurs only in characters 10, 12 and 19. In *S. falcatus*-group species there are apotypic states and character changes in all multistate characters, including those not listed because of missing data points.

This trend is particularly true in characters of the female genitalia. Female genitalia are rather uniform overall among *S. lateralis*-group species, but undergo markedly more evolution in the *S. falcatus*-group. Each species of the *S. falcatus*-group is diagnosed by its combination of plesio- and apotypic states, in those species where all female genital character states are known. An examination of female genital characters without missing data points (no.s 2, 7, 8, 16, 28, 29, 31, 35, 36, 38, 44, 46 and 52) yields results similar to examination of multistate characters. In *S. lateralis* group species there is an apotypic state only in character 2 and no character changes, while in *S. falcatus*-group species there are apotypic states in all characters and change occurs in all characters except 7.

These two trends are not entirely due to greater diversity of the *S. falcatus*-group. A comparison of similar sized clades, the *S. lateralis*-group versus the other three taxon clade (*S. circumflexus* + *S. neomexicanus* + *S. falcatus*), gives the same result. Each of the three species in the latter group have an autapotypic feature, while the species of the *S. lateralis*-group have none. The initial dichotomy in the *S.*

circumflexus + *S. neomexicanus* + *S. falcatus* clade is supported by six synapotypies, two of which (characters 46, 47) are not exhibited in any other dichotomy. This is not true of any dichotomy within the *S. lateralis*-group. Any species in the *S. circumflexus* + *S. neomexicanus* + *S. falcatus* clade differs from the others by at least four apotypic states. The maximum number for any *S. lateralis*-group species is two.

Differences between the two species groups imply a difference in the types of selective forces operating in them. Apparently, less structural divergence has been associated with speciation events in the *S. lateralis*-group. Speciation may have been accompanied by habitat or behavioral shifts that have minimally effected the structure of *S. lateralis*-group species, which we have no information on. For example, both European species, *S. lateralis* and *S. eugeni*, have been collected at the same sites and reared from *Anthophila fabriciana* (L.), but no information is available on how these species might be partitioning this common host. This kind of information is also lacking for other species in the genus.

Differences in evolution of female genitalia between the species groups may be related to importance of host shifts in speciation, since differences in female genitalia are related to differences in host use. It is possible that speciation in the *S. falcatus*-group is accompanied by larger ecological or taxonomic changes in host type than in the *S. lateralis*-group, although there are no data to support this hypothesis. The only two species of the *S. falcatus*-group for which host data are known are allopatric sister species *S. neomexicanus* and *S. falcatus*. Both attack sod-living noctuid larvae, but may do so in a different manner. *S. falcatus* parasitizes a moderately wide range of species in various habitats, and this range might be different than that of *S. neomexicanus*. *S. lateralis* and *S. eugeni* have been reared from a common host, but *S. lateralis* has been reared from a wide taxonomic range of other species, and the third member of the *S. lateralis*-group, *S. papilionae* has been reared from a macrolepidopteran. Much more rearing of *Sathon* species is necessary before a coherent explanation of species group differences can be made.

This observed difference in evolutionary trends, along with the branching pattern of the reconstructed phylogeny, forms the basis for the organization of *Sathon* into two species groups. Two monophyletic groups are defined, each supported by synapotypies and each displaying difference in degree of divergence among component species and between one another. Especially important is the difference in genital evolution between species groups. Although little has been done to describe the genitalic variation in other members of the tribe Microgastrini (Mason 1981) it appears that this divergence of genitalia is a distinctive feature of the *S. falcatus*-group.

PHENETIC ANALYSIS

Methods

Numerous characters that vary significantly among *Sathon* species were not used to reconstruct the phylogeny of *Sathon* because of marked lability. These characters display numerous states in both *Sathon* and the outgroup, and this is considered *a priori* evidence that these characters are more changeable than characters which show only two states, despite the possibility of undetected reversals. They display considerable variation in the outgroup, some displaying as wide a range of states or wider in the six *Choeras* species as is found in *Sathon*. Polarization of such characters was not possible with any degree of confidence. These characters, listed in table 3, also displayed a greater amount of incongruency because of their lability, among themselves and when compared as a group to the characters in table 1. This is apparently a straightforward correlation between frequency of change and likelihood that a character state would arise more than once.

Whether or not such characters are useful as indicators of phylogeny, they do contain information about degree of divergence between *Sathon* species and character evolution. This kind of information is interesting with reference to reconstructed phylogenetic relationships, especially when degree of divergence and proximity of phylogenetic relationship are not correlated. Therefore, these characters, along with the polarized characters, were subjected to phenetic analysis, where polarization and other evolutionary considerations are not of great methodological importance. In the following analysis, no attempt is made to propose an alternative hypothesis about relationships within *Sathon*. Rather, this analysis is used primarily to illustrate interesting differences between *Sathon* species and especially species groups, *given* tentative acceptance of the phylogenetic hypothesis drawn in the preceding section. All conclusions drawn in this section are considered of interest only in light of this phylogeny.

The characters of tables 1 and 3 are analysed with the Taxmap program, which is discussed by Carmichael and Sneath (1969). Taxmap is a computer-operated program which performs a proximity analysis of OTU's (operational taxonomic units that can be defined as individuals, species, higher taxa, *etc*. In this study OTU's are *Sathon* species). It also performs a cluster analysis using very sophisticated criteria (Carmichael, George and Julius 1968). This program was used both because of its sophistication, and its ease of use and versatility. Binary, multistate unordered, multistate ordered and continuous (morphometric) characters can be used. Analysis may be unweighted, or weighted on the basis of the amount of information (approximately the number of states occurring) each character contains.

A taxometric map (fig. 138) is produced using the proximity analysis (tables 4 and 5) and clustering information. This is a two-dimensional representation of the clusters, with circles expressing cluster size and lines between clusters representing linkage distance. Only the closest links are displayed, with arrows on the lines indicating the nearest neighbor of each cluster. Emphasis is given to the closest links to reduce distortion occurring when multidimensional relationships are graphically reduced to two dimensions (Carmichael and Sneath 1969). The primary disadvantage of a taxometric map is that an ordination of species, such as that provided by a cladogram, is not produced. This makes a comparison of relationships between the reconstructed phylogeny and phenetic analysis more difficult, but it is compensated for by the more accurate depiction of phenetic distances between clusters. To facilitate comparison between the two methods, a diagram of phenetic linkages is displayed adjacent to the reconstructed phylogeny (fig. 139).

Characters

Characters used in phenetic analysis only are listed in table 3. Since characters in both tables 1 and 3 are used in this analysis, the characters of table 3 are numbered consecutive to those of table 1. Species are arranged in phylogenetic order to be consistent with table 1. States of characters in table 3 are given number codes, as required by the taxmap program, and states of table 1 characters are recoded numerically. States are ordered into transformation series based on degree of morphological similarity whenever possible. For most characters in table 1, state **a** becomes state 0, state **b** becomes state 1, etc., with primes being eliminated by reordering of states or by coding independently derived states the same. Exceptions occur for characters in which there is a negative state. These characters involve degrees of development of length, sculpture, etc., where the least developed state is not considered the plesiotypic state and is coded **-b**. Here, **-b** becomes state 0, state **a** becomes state 1, state **b** becomes state 2 and so on.

An example of recoding is provided by character 12, propodeum sculpture. State **12-b** (smooth) becomes state 0, state **12a** (wrinkled) becomes state 1, state **12b** (lateroapically rugose) becomes state 2 and state **12b'** (areolate-rugose) becomes state 3. All states are ordered by degree of similarity although this has the effect of ignoring character evolution. For example, states **12b** and **12b'** are phenetically similar and increase estimates of similarity between species with these states, even though I hypothesize that they are independently derived.

Phenetic Affinities

Dissimilarity matrices generated by the taxmap program are given in tables 4 (weighted analysis) and 5 (unweighted). Numbers listed give an index of what proportion of states of all characters differ between each pair of compared species. Weighted and unweighted analyses gave very similar results. The information from the weighted matrix (table 4) was used by the clustering algoritm to find clusters and to create the taxometric map (fig. 138). A linear arrangement of species was also produced, based on phenetic relationships (fig. 139), to display a comparison between phenetic and phylogenetic links.

In both analyses, the only multispecies cluster is the *S. lateralis*-group. As seen from the uppermost three sets of distances in both half table 4 and 5, the three

Table 3. Characters used in Taxmap Analysis.

For explanation of characters see text. Characters are numbered consecutive to table 1. lat = *S. lateralis*, pap = *S. papilionae*, eug = *S. eugeni*, lev = *S. laevidorsum*, agg = *S. aggeris*, mas = *S. masoni*, cin = *S. cinctiformis*, cir = *S. circumflexus*, neo = *S. neomexicanus*, fal = *S. falcatus*.

Characters	lat	pap	eug	lev	agg	mas	cin	cir	neo	fal
54. Oral plate dorsal margin	1	0	1	–	–	2	0	3	0	3
0 = concave										
1 = flat, desclerotized										
2 = flat										
3 = convex										
55. Pronotal groove sculpture	1	1	1	0	1	3	3	0	2	2
0 = smooth										
1 = ventral groove sculptured										
2 = dorsal and ventral groove sculptured										
3 = grooves foveolate										
56. Ventral polished band shape	1	0	0	0	0	0	0	1	1	1
0 = ant. narrowed										
1 = bottle-shaped										
57. Ventral groove width	1	0	2	0	0	1	1	0	0	0
0 = narrow										
1 = widened										
2 = wide										
58. Disc seta length	1	1	0	0	0	0	0	0	0	0
0 = short										
1 = long										
59. Disc seta distribution	0	1	1	0	0	0	1	0	1	1
0 = sparse ventrally										
1 = uniform										
60. Mesoscutal seta pattern	0	0	1	1	0	1	0	0	1	0
0 = medially convergent										
1 = post. directed										

(continued on next page)

Table 3 (continued)

Characters	lat	pap	eug	lev	agg	mas	cin	cir	neo	fal
61. Prescutellar furrow width 0 = narrow 1 = widened 2 = very wide	0	0	0	0	1	2	1	0	1	1
62. Prescutellar furrow sculpture 0 = medially absent 1 = medially obscure 2 = complete	1	1	1	1	0	2	1	1	1	1
63. Scutellar costae 0 = obscure medially and anteriorly 1 = obscure medially 2 = complete	1	1	1	1	1	2	2	0	2	0
64. Scutellar anterior groove margin 0 = indistinct 1 = distinct	1	0	0	0	0	1	0	1	0	1
65. Scutellar dorsal groove width 0 = narrow 1 = post. narrowed 2 = wide	1	1	1	0	1	2	2	2	2	2
66. Metasomal lateral pit shape 0 = narrow, with anterior margin 1 = wide, without anterior margin	0	1	1	0	0	1	0	1	0	0
67. Metapleural groove 0 = absent 1 = smooth 2 = foveolate	1	1	1	0	0	2	2	1	1	1
68. Propodeal spiracle shape 0 = round 1 = oval	1	0	0	0	1	0	0	1	1	1

(continued on next page)

Table 3 (continued)

Characters	lat	pap	eug	lev	agg	mas	cin	cir	neo	fal
69. Leg color	1	1	1	1	1	0	0	0	0	0
0 = unicolorous										
1 = infuscate										
70. T1 shape	0	0	0	0	4	1	3	1	2	2
0 = evenly narrowed, narrow										
1 = evenly narrowed, wide										
2 = apically narrowed										
3 = widened, narrow apex										
4 = widened										
71. Third valvula apex size	1	1	1	1	0	0	1	0	1	0
0 = small										
1 = large										
72. Third valvula apex shape	0	1	0	0	0	0	1	1	0	1
0 = acute										
1 = emarginate										

species of the *S. lateralis*-group are the most closely linked in the genus, more so than sister species *S. laevidorsum* + *S. aggeris* (dist. 267 weighted, 243 unweighted) and *S. masoni* + *S. cinctiformis* (dist. 196 weighted, 217 unweighted). This cluster, cluster 1, is given as the only circle of positive radius on the taxometric map (fig. 138), all other clusters being single points without radius.

In the *S. falcatus*-group each species is placed in its own single member cluster. The dissimilarity matrix and taxometric map show that sister species display close phenetic similarity. However, none of these species pairs are similar enough to be clustered together when measured against the relative cohesiveness of the *S. lateralis*-group. Nearest neighbors are *S. laevidorsum* + *S. aggeris*, *S. masoni* + *S. cinctiformis* and *S. circumflexus* + *S. falcatus* with *S. neomexicanus* also closely linked to *S. falcatus*. At a lower level of linkage, *S. laevidorsum* and *S. aggeris* are more similar to the *S. lateralis*-group species than to the rest of the *S. falcatus*-group, while *S. masoni* and *S. cinctiformis* are linked to *S. circumflexus* + *S. falcatus* + *S. neomexicanus* (figs. 138, 139).

Figure 139 displays the order of links in phylogenetic versus phenetic systems. Line lengths do not indicate degree of divergence in either system. Lines serve only

Table 4. Dissimilarity matrix from taxmap program, weighted analysis
lat = *S. lateralis*, pap = *S. papilionae*, eug = *S. eugeni*, lev = *S. laevidorsum*, agg = *S. aggeris*, mas = *S. masoni*, cin = *S. cinctiformis*, cir = *S. circumflexus*, neo = *S. neomexicanus*, fal = *S. falcatus*.

Taxa	lat	pap	eug	lev	agg	mas	cin	cir	neo
pap	123								
eug	146	098							
lev	281	272	293						
agg	323	386	418	267					
mas	408	428	386	435	453				
cin	465	424	424	502	466	196			
cir	438	414	443	460	529	330	408		
neo	489	454	424	494	577	385	350	266	
fal	524	490	519	559	587	421	438	185	202

Table 5. Dissimilarity matrix from taxmap program, unwieghted analysis
lat = *S. lateralis*, pap = *S. papilionae*, eug = *S. eugeni*, lev = *S. laevidorsum*, agg = *S. aggeris*, mas = *S. masoni*, cin = *S. cinctiformis*, cir = *S. circumflexus*, neo = *S. neomexicanus*, fal = *S. falcatus*.

Taxa	lat	pap	eug	lev	agg	mas	cin	cir	neo
pap	133								
eug	169	102							
lev	297	282	297						
agg	333	383	420	243					
mas	424	434	383	416	452				
cin	480	424	424	482	481	217			
cir	440	421	457	468	518	321	400		
neo	495	471	425	483	573	380	359	262	
fal	520	494	530	557	580	420	436	186	215

to display the *order* in which species are connected, with information on morphological divergence given in the dissimilarity matrix and the taxometric map (fig. 138). Linkage order for the phenetic system was estimated from the dissimilarity martices. There are several points of incongruity between the phylogenetic reconstruction and phenetic analysis. These points illustrate both interesting features about the evolution of *Sathon* species and basic weaknesses in phenetic systems of relationship analysis. All of the areas of incongruence can be seen to be due to factors in character evolution that phentic systems do not analyse.

Both weighted and unweighted analyses show that links for *S. laevidorsum* and *S. aggeris* are closest with one another, then with members of the *S. lateralis*-group, then with *S. masoni*. Links for *S. masoni* and *S. cinctiformis* are closest with one another, then with *S. circumflexus* and *S. neomexicanus*, then with *S. lateralis*-group species. The closest linkage of the *S. lateralis*-group species in the *S. falcatus*-group is with *S. laevidorsum*. The closest links of species in the *S. circumflexus* + *S. neomexicanus* + *S. falcatus* clade are first with one another, then with *S. masoni* + *S. cinctiformis*, then with the *S. lateralis*-group. This is not totally congruent with the phylogenetic branching pattern (fig. 139). The phenetic similarity between the *S. lateralis*-group and *S. laevidorsum* + *S. aggeris* supports the hypothesis that the latter two species are relatively plesiotypic within their species group, since this similarity is primarily due to symplesiotypy (see characters of table 1, most of which display state a in the *S. lateralis*-group and *S. laevidorsum* + *S. aggeris*).

Another point of incongruence between the reconstructed phylogeny and phenetic analysis is the placement of *S. circumflexus* and *S. falcatus* as nearest neighbors, with *S. neomexicanus* linked to its sister species at a greater distance than *S. circumflexus*. The phenetic distance between *S. neomexicanus* and its sister species is caused by the presence of numerous states unique to *S. neomexicanus* within the *S. circumflexus* + *S. neomexicanus* + *S. falcatus* clade. These are especially prevalent among unpolarized characters (table 3, characters 54, 60, 63, 64, 71 and 72), and may represent unique apotypic states or retained plesiomorphies. Hence, *S. neomexicanus* is phenetically divergent from *S. circumflexus* and *S. falcatus*, although there are not an exceptionally high number of apotypies listed for this species on the cladogram (fig. 137).

Most comparisons show agreement between the two methods. All other sister species and sister group relationships are supported phenetically. The order of links among *S. lateralis*-group species is the same in both phenetic and phylogenetic analyses. Based on the order of linkages, a linear ordination of species is the same between the two methods except for the placement of *S. neomexicanus* and *S. falcatus* (fig. 139). The difference in clustering between the *S. lateralis*- and *S. falcatus*-groups is the most important congruency between the phylogenetic and phenetic analyses. As stated in the preceding chapter, members of the *S. lateralis*-group display few apotypies and few character changes, with a high degree of similarity in habitus among species. Members of the *S. falcatus*-group are distinctive, with numerous autapotypies, and are easily separated even from sister species. In spite of the addition of numerous unpolarized characters that display many incongruences with the cladogram, this difference in character evolution between the species groups is preserved and quantified in the phenetic analysis. Although phenetic analysis is not useful as a primary method of indicating relationships between taxa, it has given evidence supporting the classification of *Sathon* species into two species groups, reinforced hypothesized relationships between species, and illustrated some features of the evolution of the genus.

ZOOGEOGRAPHIC ANALYSIS

A zoogeographic study is an attempt to understand patterns in the distribution of animals, and how these patterns came about (Darlington 1957). The distributions of species are examined, and correlated with past geological and climatological events that may have affected the distributions of species under study or their ancestors. The most fruitful analyses are based on reconstructed phylogenies, in which evolutionary and geographical relationships among species are both considered (Nelson and Platnick 1981). Performing this analysis on the geographical and evolutionary history of *Sathon* is difficult. Like most Braconidae, few species have been collected extensively. Ranges, the basic data of biogeographic study, are certainly inadequately known for most *Sathon* species. Most species are known from short series of specimens from one or a few localities. This makes interpretation of distribution patterns in *Sathon* uncertain. Additionally, there is no fossil record for the genus. The only fossil microgastrine known is *Eocardiochiles* Brues, a very plesiotypic genus overall, whose relationships with extant Microgastrinae are unknown. It is certainly not closely related to *Sathon*. Although the age of this fossil from Baltic amber is known (late Eocene or Oligocene) it is of little practical use in inferring a date of origin for *Sathon*. This creates a basic problem in correlating speciation events in *Sathon* with past geological or climatological events.

An understanding of the geographical distribution of groups related to a taxon is often of benefit in finding its possible area of origin (Udvardy 1969). This method is of little use in *Sathon* biogeography, however, since *Choeras* is an inadequately known, cosmopolitan genus whose phylogenetic relationship with *Sathon* is unclear. The systematics and biogeography of *Choeras* remain unstudied.

The centre of origin of *Sathon* can be inferred only from the present distributions of *Sathon* species, using the assumption that the range of the ancestor of the genus is contained within or represented by the ranges of its descendant species (Darlington 1957, Udvardy 1969). *Sathon* is primarily Holarctic. The only exception is *S. aggeris*, a structurally aberrant species from South America. Given that the initial speciation event in *Sathon* probably resulted in a North American ancestor of the *S. falcatus*-group and a Palaearctic ancestor of the *S. lateralis*-group, then the ancestor was either Holarctic initially or dispersed between continents after arising on one of them. The progression rule (Hennig 1966, Brundin 1966) hypothesizes that phylogenetically plesiotypic species are closer to the ancestral range. Phenetically, the most plesiotypic species in *Sathon* is the European *S. lateralis*, and the most plesiotypic species group is the primarily Palaearctic *S. lateralis*-group. Dispersal from the Palaearctic to the Nearctic Region could have occurred either through the Bering land bridge or from Europe into North America, since both routes were open for long periods of time (Matthews 1979). However, the ancestors of the *S. lateralis*- and *S. falcatus*-groups arose at the same time in the first speciation event within the genus. Although the *S. lateralis*-group is phenetically more plesiotypic than the *S. falcatus*-group, it is not so phylogenetically and therefore cannot be used as an indicator since both species groups are of the same age.

A more useful hypothesis is that the ancestor of *Sathon* may have been Holarctic. If we accept the vicariance hypothesis that the range of a species must be continuous for that species to retain its unity, and that long distance dispersal between Europe and North America was unlikely after the opening of the North Atlantic ocean (Nelson and Platnick 1981), then the ancestor of *Sathon* would have had a Laurasian distribution. The initial speciation event in the genus would have been due to the splitting of this range, perhaps by inundation of land connections between North America, Greenland and Europe. Several such connections were in existence until the Eocene, with one between Greenland and Scandinavia possibly lingering until the Miocene (McKenna 1972, Talwani and Udintsev 1977).

No matter which hypothesis is chosen, subsequent differentiation of North American and Palaearctic populations occurred, giving rise to the first speciation event of *Sathon* phylogeny (fig. 137, dichotomy A, Fig. 142).

The ancestor of the *S. lateralis*-group was probably Palaearctic, since two of its three *S. lateralis*-group species are European. The presence of *S. papilionae* in North America is probably due to dispersal. The geographical events coincident with the speciation event that gave rise to *S. lateralis* and the ancestor of *S. papilionae* + *S. eugeni* are unknown. *S. lateralis* and *S. eugeni* are broadly sympatric. All *S. lateralis*-group species occur in areas where habitat distributions have been markedly affected by Pleistocene glaciations (Turekian 1971) and geographical evidence of the initial speciation event has probably been obscured by these range fluctuations. The distribution of *S. papilionae* on the west coast of North America leads to the speculation that the ancestor of *S. papilionae* + *S. eugeni* may have dispersed to North America via the Bering land bridge. This connection existed for a long period of time, from the Late Cretaceous to the Pliocene, and again in the Pleistocene (Hopkins 1967), so an approximate date for the invasion of the *S. lateralis*-group into North America cannot be given. Subsequent inundation of the Bering Strait, resulting in the isolation of Nearctic and Palaearctic populations, would have given rise to *S. papilionae* and *S. eugeni*. This hypothesis leads to the prediction that further collecting in the eastern Palaearctic region might reveal the presence of *S. eugeni* or other *S. lateralis*-group species closely related to *S.*

papilionae which are currently unknown. This would fill in the rather wide geographical gap between western Europe and Alaska, an area from which no specimens of *S. lateralis*-group species are known.

The ancestor of the *S. falcatus*-group appears to have been Nearctic. Five of seven known *S. falcatus*-group species occur in North and Central America. This includes *S. laevidorsum*, the most plesiotypic species overall in the *S. falcatus*-group. *S. laevidorsum* has the fewest apotypic character states of any *S. falcatus*-group species (table 1), and is very similar in habitus to *S. lateralis*-group species. Presence of *S. falcatus* group species on other continents is apparently due to dispersal.

The first speciation event in the *S. falcatus*-group may have been caused by north-south vicariance in North America (including México). This would result in a southern ancestor of *S. laevidorsum* + *S. aggeris*, and a northern ancestor of the remainder of the *S. falcatus*-group. This was apparently followed rather quickly (in geological time) by the dispersal of the southern species into South America, either by island hopping or over the Isthmus of Panamá once this was established in the Pliocene (Rosen 1975, Raven and Axelrod 1975). Another vicariant event may have occurred relatively soon afterward, giving rise to *S. laevidorsum* in Central America and *S. aggeris* in South America. This may be related to the movement of the Caribbean islands to their present positions from a bridging position in the area of the present-day isthmus (Rosen 1975). The relative antiquity of these events is indicated by overall plesiotypy of these two species in the balance of their characters. Also, the large number of autapotypies superimposed on a plesiotypic ground plan in *S. aggeris* suggest long isolation from other *Sathon* species, assuming all evolutionary rates to be equal. Support for this hypothesis might be gained if the *Sathon* fauna of South America were more intensively studied. It would be expected that speciation in South America would have kept pace with that in North America if the ancestor of *S. aggeris* had been isolated for a long time. The result would be a monophyletic lineage related to *S. aggeris*, of which *S. aggeris* is the only known representative. The braconid fauna of South America is very inadequately known, and the probability of the existence of unknown *Sathon* species is quite high.

The northern fragment of the *S. falcatus*-group ancestor gave rise to two species in North America, the ancestor of *S. masoni* + *S. cinctiformis* and the ancestor of *S. circumflexus* + *S. neomexicanus* + *S. falcatus*. The geographical component of this speciation is obscure. All North American species have probably undergone considerable range fluctuations during Pleistocene glaciations, which may have concealed vicariance events. Additionally, one of the extant results of North American speciation events, *S. neomexicanus*, has become transcontinental since the last glaciation, establishing sympatry with all North American species. This further obscures geographic patterns for those speciation events which had a geographical component. The only piece of information that can be noted is that both *S.*

circumflexus and *S. neomexicanus* occur in the American southwest (*S. circumflexus* exclusively so), while neither *S. masoni* or *S. cinctiformis* occur there. Possibly the ancestor of *S. circumflexus* + *S. neomexicanus* + *S. falcatus* arose in southwestern United States as the result of some range division.

A habitat shift may have been involved also, although information supporting this is scanty. While no information is available for *S. masoni*, there are specimens of its sister species, *S. cinctiformis*, with label data indicating collection at several localities from marshy areas dominated by sedges. In contrast, specimens of both *S. circumflexus* and *S. neomexicanus* have been collected from meadows, with a preference for high altitudes or high latitiudes. *S. neomexicanus* has been reared from grass-eating noctuids. An east-west vicariance dividing the range of an apparently transcontinental ancestral species may have occurred also, resulting in a southwestern, meadow-living ancestor of *S. circumflexus* + *S. neomexicanus* + *S. falcatus* and an eastern, marsh-living ancestor of *S. masoni* + *S. cinctiformis*. Unfortunately, the ancestral habitat is unknown. There is little information on habitat preference for plesiotypic *S. falcatus*-group species. *S. laevidorsum* and *S. aggeris* were taken from high-altitude localities in México and Ecuador that may have no resemblance to habitats of North American species. Therefore, it is difficult to state whether the meadow or marsh habitat was ancestral, and lack of information on ecological plasticity prevents understanding of how useful such limited habitat information might be. Certainly several species of *Sathon*, among them *S. falcatus*, have wide ranges of host preference. This may be an indicator of ecological plasticity in *Sathon* species.

The current distribution of sister species *S. masoni* and *S. cinctiformis* display apparent refugial effects. *S. cinctiformis* is a primarily southeastern species, which probably survived the last glaciation south of the ice. *S. masoni* is a northwestern species found primarily in Alaska, although collecting of this species has been too inadequate to make firm statements about the southern limits of its range. *S. masoni* appears to have survived the last glaciation in the Beringian refugium (Matthews 1979), with subsequent dispersal southward at the end of the Wisconsinan glaciation period. These two species may be the result of an east-west vicariance event, perhaps related to climatic fluctuation. Refugial isolation of two populations of the ancestor may have been responsible for speciation, but since several glacial events have been hypothesized for North America (Turekian 1971) it is difficult to assign a date to this occurrence.

Nothing is known about the geographic events, if any, involved in the separation of the ancestor of *S. circumflexus* + *S. neomexicanus* + *S. falcatus* into two species. *S. circumflexus* and *S. neomexicanus* are site-sympatric, and the range of *S. circumflexus* is contained entirely within the range of *S. neomexicanus*. It is not known why *S. neomexicanus* could be so plastic ecologically as to be found over most of Canada and the United States but *S. circumflexus* be limited to three southwestern states. *S. falcatus*, the other member of this clade, is also transcontinental in the Palaearctic region. Apparently, the ancestor of *S. neomexicanus* + *S. falcatus* had this trait of vagility and adaptability that is not found in its sister species *S. circumflexus*, assuming that there is no collecting bias. A difference in range of host preference may be involved, but there is no evidence to support this possibility.

The presence of *S. falcatus* in the Palaearctic region is probably due to dispersal. The large number of apotypic states shared by *S. neomexicanus* + *S. falcatus* indicates a long common history, and the dispersal of the ancestor of *S. neomexicanus* + *S. falcatus* into Europe is probably the most recent event in the geographic history of the genus. It seems very likely that this dispersal occurred long after the loss of a land connection between North America and Europe, and that dispersal likely occurred through Beringia. It is not known, however, whether this dispersal occurred in the Pliocene or more recently, during the Pleistocene. Inundation of the Bering Strait would result in speciation and the modern distributions. Both *S. neomexicanus* and *S. falcatus* are widely distributed in their respective continents, appearing quite capable of extensive range enlargement. As with the dispersal of *S. papilionae* into North America, an exact date for the reverse dispersal of the ancestor of *S. falcatus* is not known.

The above discussion shows that much more information is needed about ranges, habitat requirements and hosts before workable zoogeographic hypotheses can be proposed. Speciation always need not be accompanied by changes in range, especially in parasitic forms where host preferences form an important aspect of life history. The effects of refugia and pleistocene climatic fluctuations may have been a dominant factor in *Sathon* distributions. These factors have had their effects over the entire globe, even in tropical regions (Prance 1982). A better understanding of host preferences and ecological requirements may allow hypotheses on which speciation events in *Sathon* may have had geographical causes and which might be attributed to other agents. Also, this type of information may aid in understanding how ranges of *Sathon* species were effected by climatic fluctuations, and how modern ranges might be related to ancestral ones. Without such information, the scenario presented above is a very tentative estimate.

CONCLUSION

This is a preliminary study of *Sathon* Mason. The genus has been doubled in size in this study, with several species known from very little material. There is still much information to be gathered about the species, and several problems to be solved.

More information is needed about immatures and host preferences. The larvae of *Sathon* species display differences in features of the head capsule, variations in prominence of the silk press, teeth of the mandible and shape of the head capsule sclerites. They may be gregarious or solitary, and fragmentary evidence suggests different ranges of host species for plesiotypic versus apotpyic species. Information about host preference and immatures is available only for *S. lateralis*, *S. eugeni* and *S. falcatus*, with one host record each for *S. papilionae* and *S. neomexicanus*. No larval exuviae are known for *S. papilionae*. Therefore, there is information for the most plesio- and apotypic species in *Sathon*, but none for intermediate species where transformation series may exist. Much rearing of parasitized hosts is necessary to gain enough information to be useful in a systematic study, since characters based on natural history are unknown for too many *Sathon* species.

A very basic task that must be done is further collection of *Sathon* specimens. This genus has been collected inadequately in the past because of the small size of species (2 - 4mm) and their generally dark and unspectacular coloration. Specimens must be swept with an extra-fine mesh insect net or trapped with a malaise or other permanently installed trap that is effective in catching flying insects. Distributional data are fragmentary to essentially non-existent for most *Sathon* species, and habitat preferences are almost unknown. Rigorous analysis of historical geography of *Sathon* species must await much more intensive collecting, especially in the inadequately known Neotropical region.

Some problems needing solution require more thorough collection of even such a relatively well known region as North America. Two examples are available. I have mentioned above the difference in habitus between northern and southern specimens of *S. masoni*. This geographic variation remains unanalysed because of a dearth of material of this species outside of Alaska. *S. masoni* has been collected from only one locality in Canada, Fort Simpson N.W.T. Much collecting must be done in the middle and southern parts of the range of *S. masoni* before the significance of the geographic variation currently seen can be understood. *S. papilionae* provides a similar problem. This species is known from only two localities, and the two paratypes from Cold Bay, Alaska display several character state differences from the holotype from Clayoquot. Whether these differences are significant or not cannot be determined from a sample size of three.

Perhaps the most important problem needing resolution is the nature of the relationship between *Sathon* and *Choeras*. The possible paraphyly of *Choeras* relative to *Sathon* carries the attendant possibility that the two species groups of *Sathon*, which have been shown above to be markedly different from each other, may be independently derived from some *Choeras* ancestor. Distributions of character states in apotypic, primarily undescribed species of *Choeras* must be examined before the status of *Sathon* can be changed. It is hoped that this study will facilitate any future attempts at understanding the relationships between *Sathon* and *Choeras* and the relationships and evolution of *Sathon* species.

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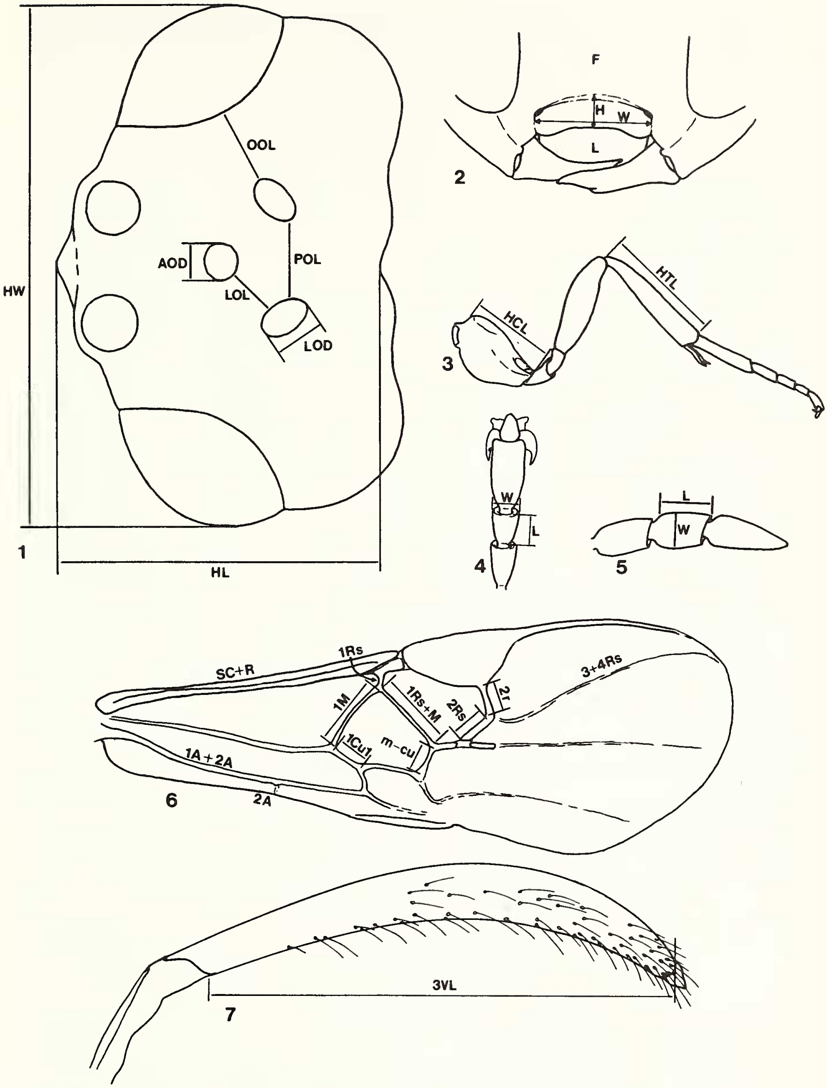
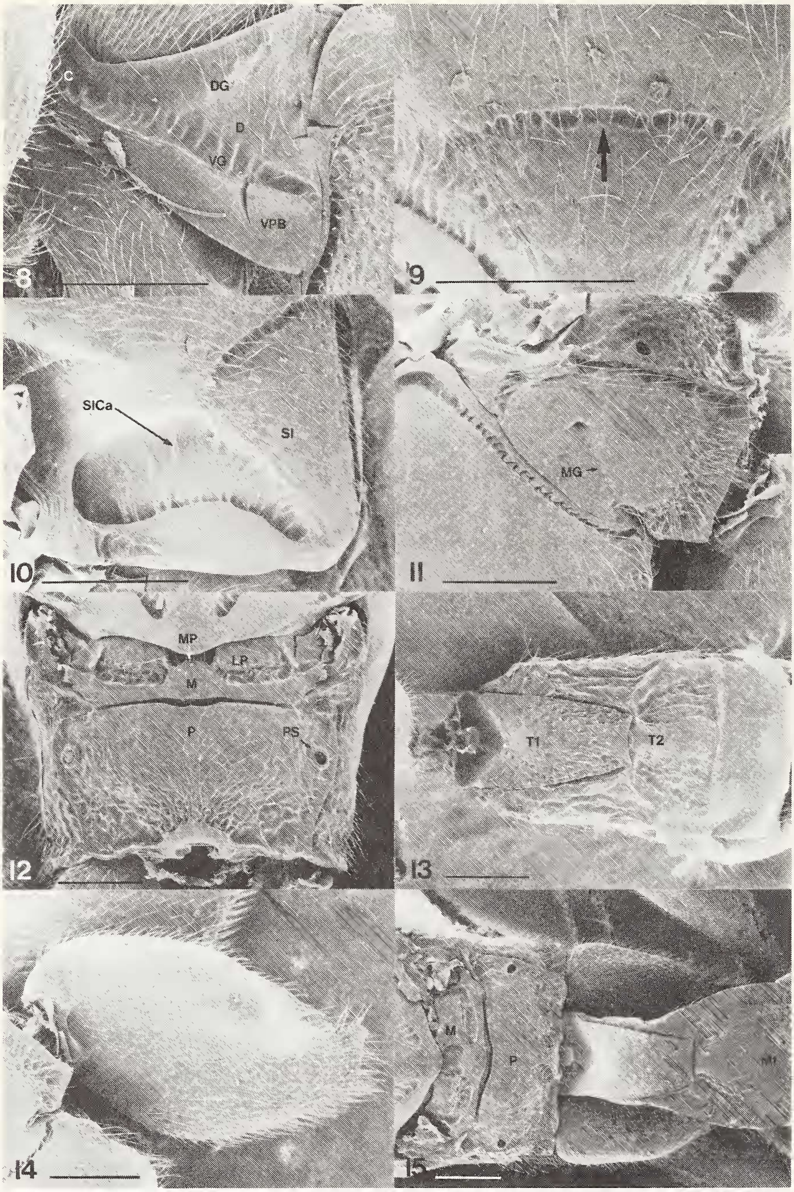
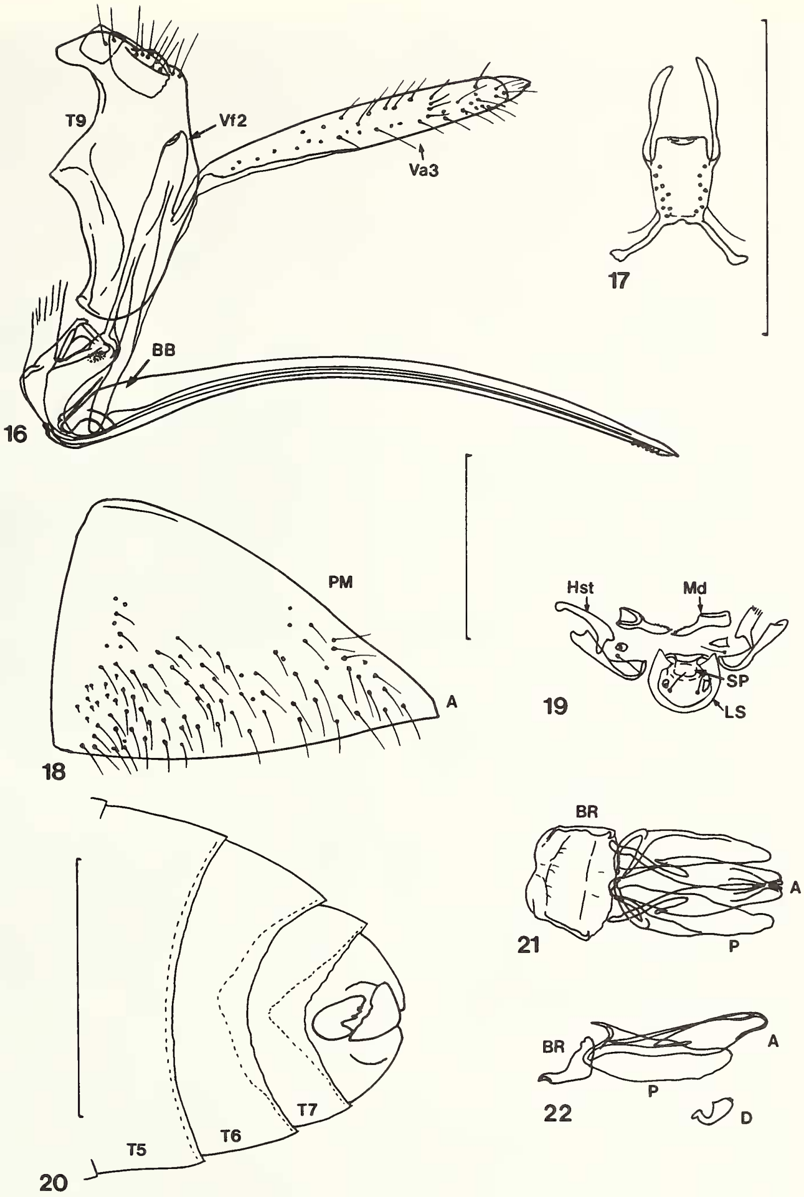
A basic set of figures is given for each *Sathon* species, covering each body part that can be used for diagnosis. Differences in arrangements among species reflects different practical considerations (see ‘Methods’). or illustration of diagnostic characters. Groups of figures for each species are arranged in the order that the species appear in the taxonomic treatment, except for figs 1 - 7. These are semidiagrammatic drawings of *S. neomexicanus* body parts which are used only as a guide to stucture names and measurement methods.



Figs. 1–7. Illustration of measurements. Body parts of *Sathon neomexicanus* drawn semidiagrammatically with all setae removed except in figure 7: 1, head, dorsal aspect (HW = head width; HL = head length; AOD = anterior ocellar diameter; LOL = lateral ocellar line; LOD = lateral ocellar diameter; OOL = ocellar-ocular line; POL = posterior ocellar line); 2, head, frontal aspect (F = frons; H = clypeus height; L = labrum; W = clypeus width); 3, hind leg (HCL = hind coxa length; HTL = hind tibia length); 4, apical foretarsomeres (L = length of penultimate foretarsomere; W = width of penultimate foretarsomere); 5, apical flagellomeres (L = length of penultimate flagellomere; W = width of penultimate flagellomere); 6, wing venation (names and approximate measuring points of wing veins used in descriptions); 7, third valvula; (3VL = length of third valvula).

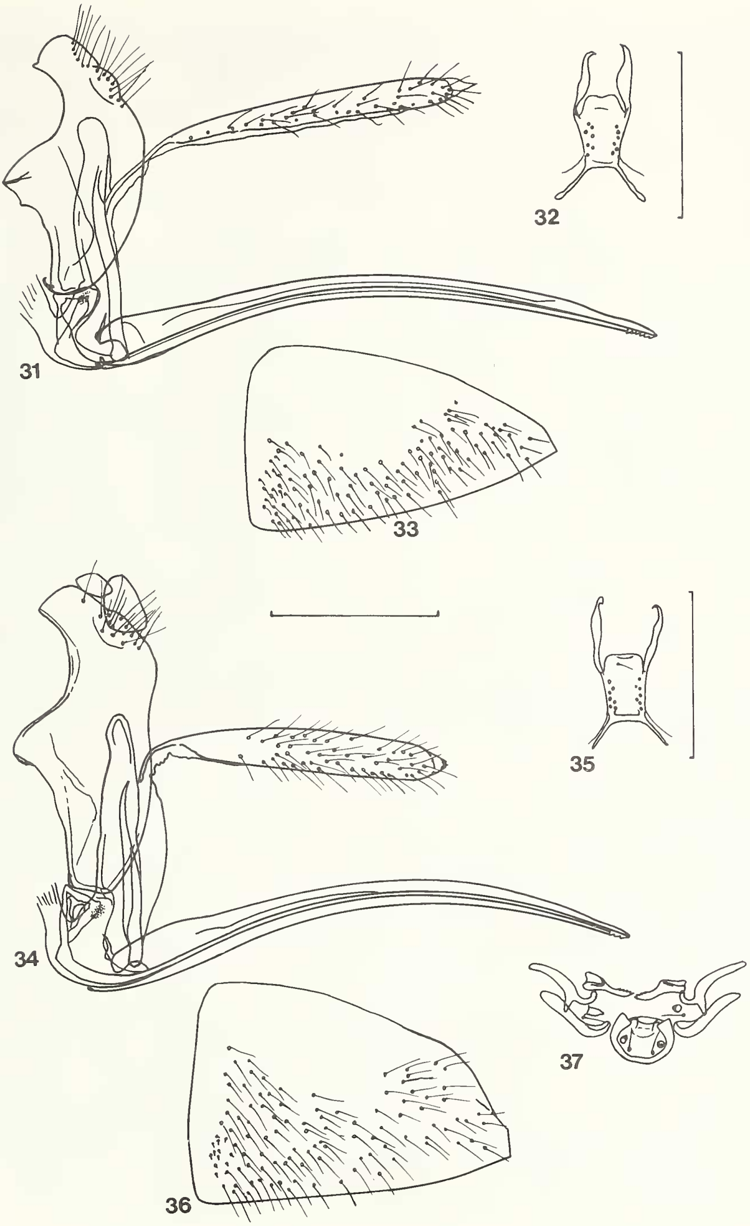


Figs. 8–15. S.E.M. photographs of *Sathon lateralis* female. Scale bars = 0.2mm: 8, pronotum, lateral aspect (C = collar; D = disc; DG = dorsal groove; VG = ventral groove; VPB = ventral polished band); 9, prescutellar furrow, dorsal aspect (arrow indicates furrow); 10, scutellum, dorsolateral aspect Sl = scutellum; Slca = scutellar costa); 11, metapleuron, lateral aspect (MG = metapleural groove); 12, metanotum and propodeum, dorsal aspect (M = metanotum; MP = medial pit of metanotum; LP = lateral pit of metanotum; P = propodeum; PS = propodeal spiracle); 13, anterior end of metasoma, dorsal aspect (T1 = first tergum of metasoma; T2 = second tergum of metasoma); 14, hind coxa, lateral aspect; 15, meso- and metasoma of male, dorsal aspect (M = metanotum; P = propodeum; Mt = metasoma).

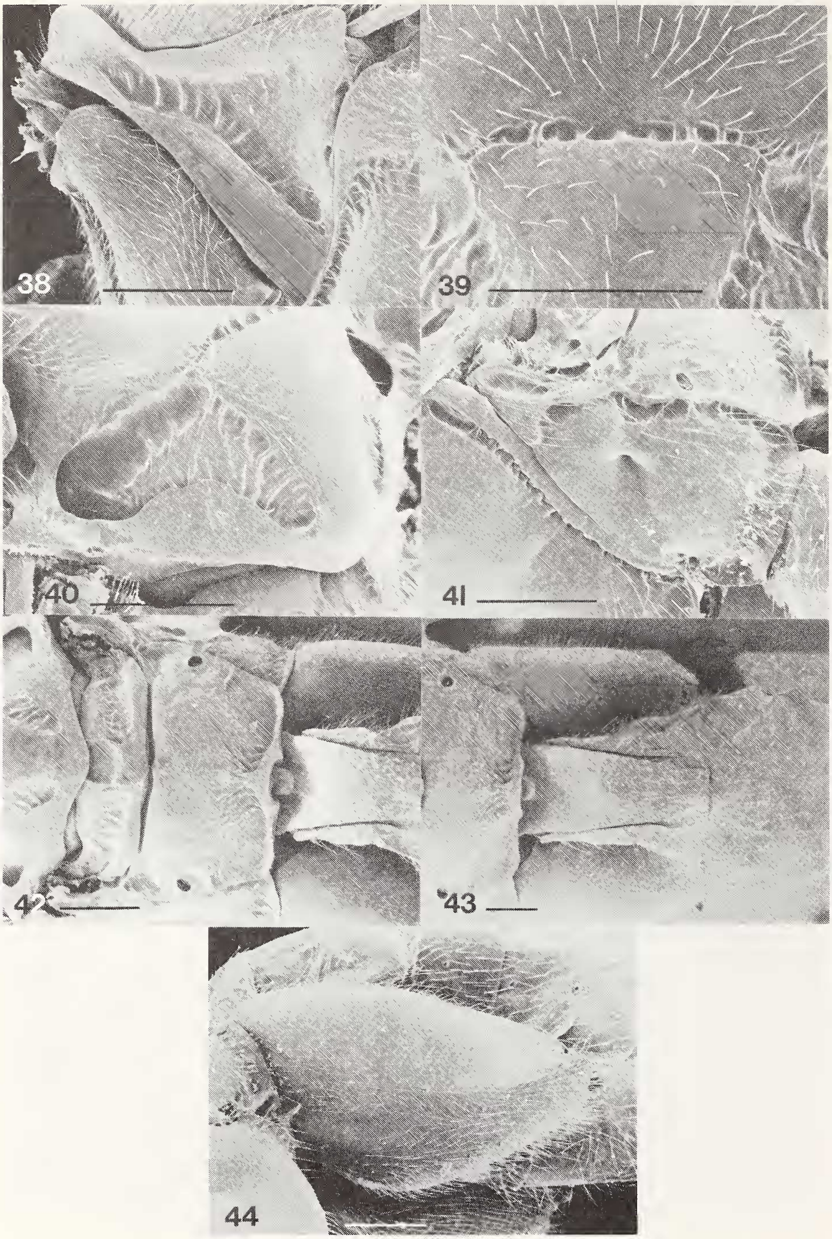


Figs. 16–22. Line drawings of *Sathon lateralis* male and female. Scale bars = 0.5mm: 16, Female genitalia, lateral aspect (BB = basal bulb of ovipositor; T9 = ninth tergum of abdomen; Va3 = third valvula; Vf2 = second valvifer); 17, oral plate of female, anterior aspect; 18, hypopygium, lateral aspect (A = apex; PM = posterodorsal margin); 19, head capsule of larva, anterior aspect (Hst = hypostoma; LS = labial sclerite; Md = mandible; SP = silk press); 20, apex of metasoma of female, dorsal aspect (T5, T6, T7 = fifth through seventh tergum of metasoma); 21, male genital capsule, dorsal aspect, volsellae removed (A = aedeagus; BR = basal ring; P = paramere); 22, male genital capsule, lateral aspect, volsellae except digitus removed (A = aedeagus; BR = basal ring; D = digitus; P = paramere).

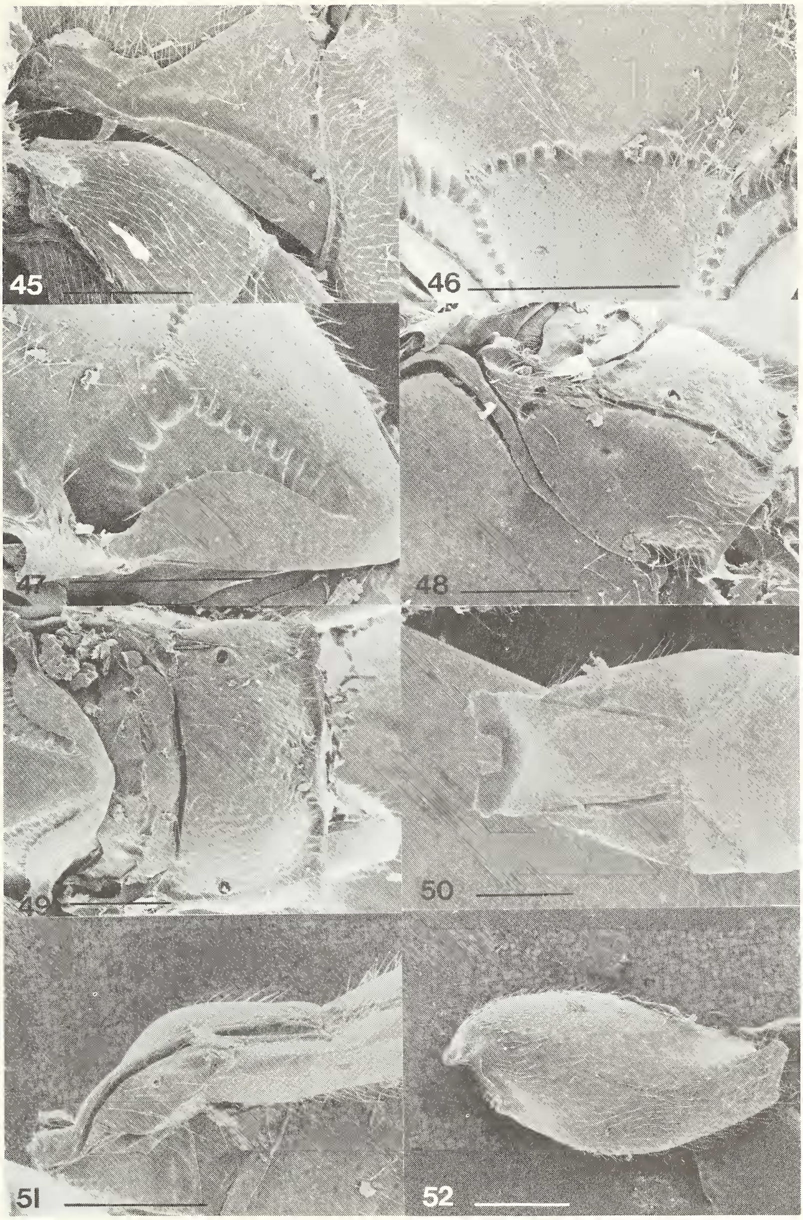
Figs. 23–30. S.E.M. photographs of *Sathon papilionae* female. Scale bars = 0.2mm except fig. 30 where scale bar = 0.05mm: 23, pronotum, lateral aspect; 24, prescutellar furrow, dorsal aspect; 25, scutellum, dorsolateral aspect; 26, metapleuron, lateral aspect; 27, metanotum and propodeum, dorsal aspect; 28, anterior end of metasoma, dorsal aspect; 29, hind coxa, lateral aspect; 30, third valvula, high magnification displaying striate microsculpture.



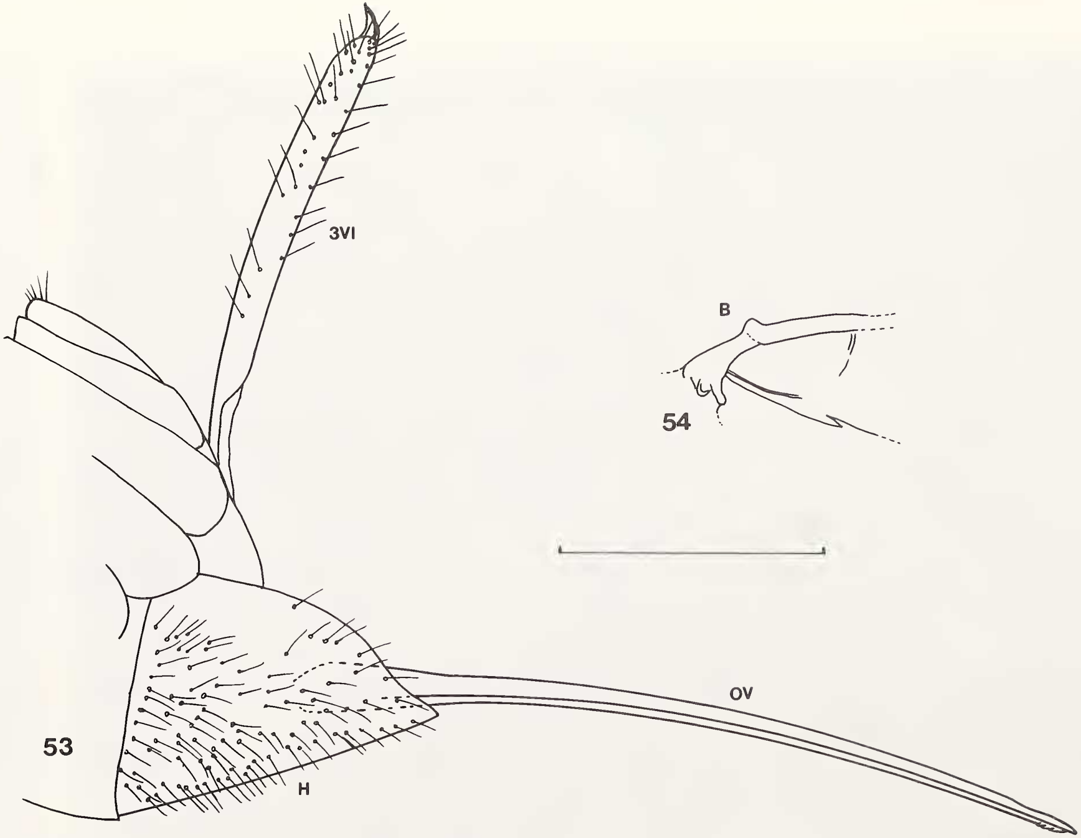
Figs. 31–33. Line drawings of *Sathon papilionae* female. Scale bars = 0.5mm: 31, female genitalia, lateral aspect; 32, oral plate, anterior aspect; 33, hypopygium, lateral aspect. Figs. 34–37. Line drawings of *S. eugeni* female. Scale bars = 0.5mm: 34, female genitalia, lateral aspect; 35, oral plate of female, anterior aspect; 36, hypopygium, anterior aspect; 37, head capsule of larva, anterior aspect.



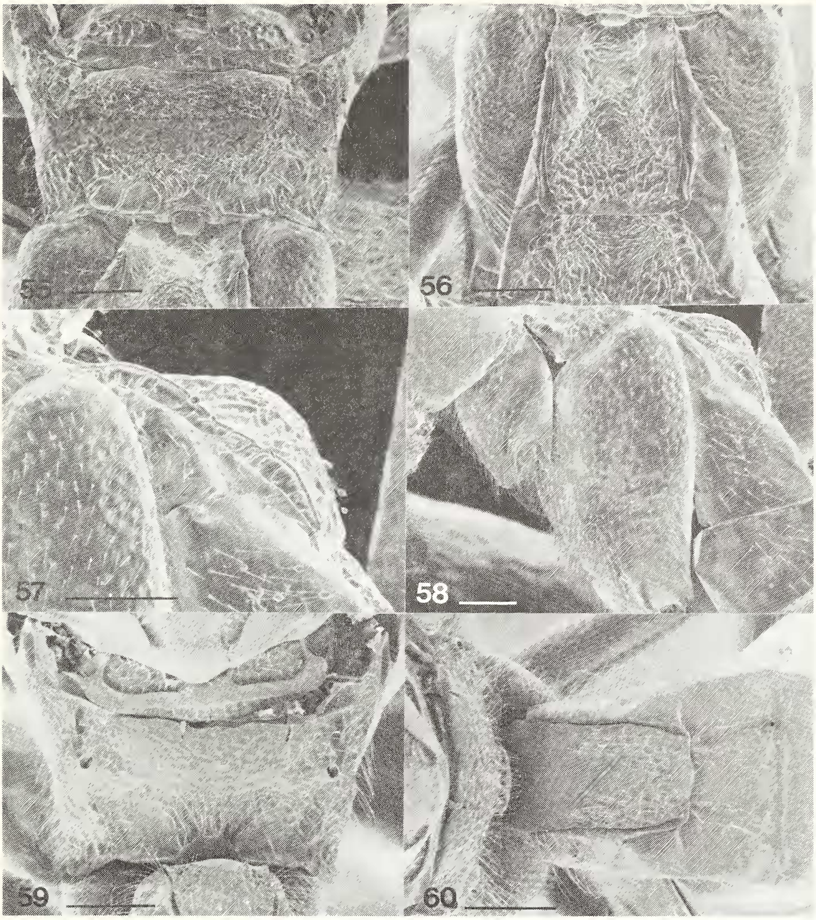
Figs. 38–44. S.E.M. photographs of *Sathon eugeni* female. Scale bars = 0.2mm: 38, pronotum, lateral aspect; 39, prescutellar furrow, dorsal aspect; 40, scutellum, dorsolateral aspect; 41, metapleuron, lateral aspect; 42, metanotum and propodeum, dorsal aspect; 43, anterior end of metasoma, dorsal aspect; 44, hind coxa, lateral aspect.



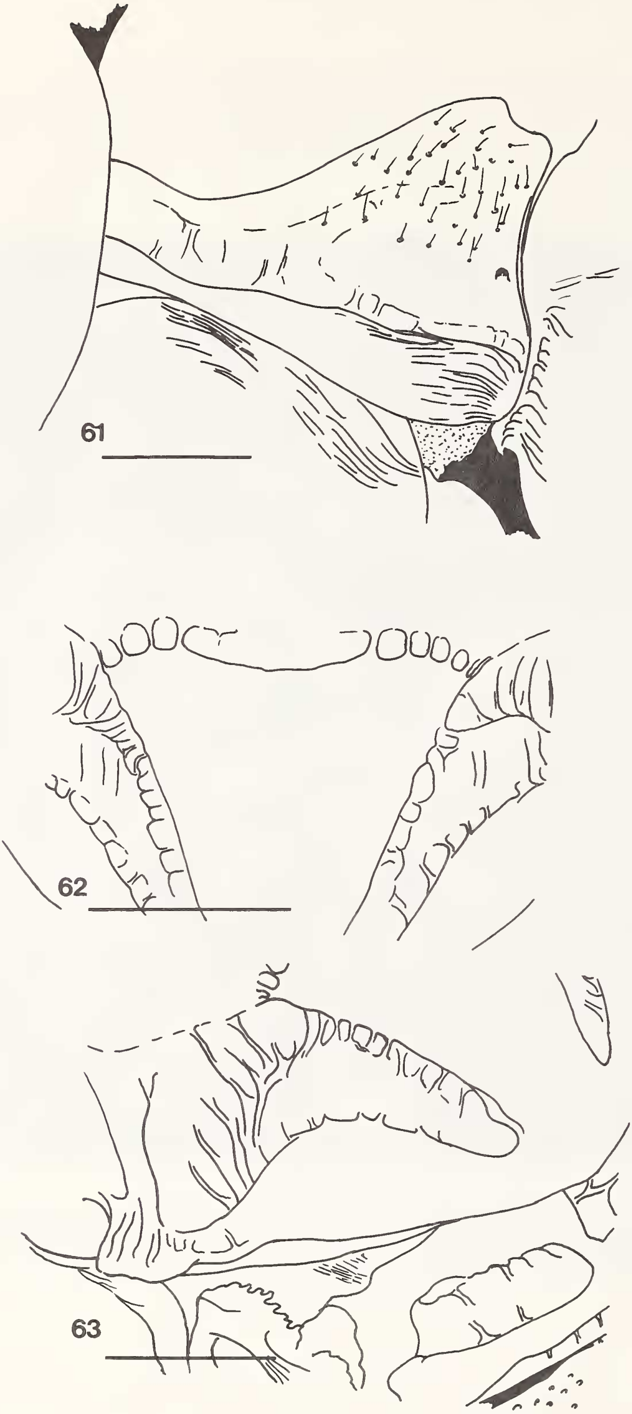
Figs. 45–52. S.E.M. photographs of *Sathon laevidorsum* female. Scale bars = 0.2mm: 45, pronotum, lateral aspect; 46, prescutellar furrow, dorsal aspect; 47, scutellum, dorsolateral aspect; 48, metapleuron, lateral aspect; 49, metanotum and propodeum, dorsal aspect; 50, anterior end of metasoma, dorsal aspect; 51, anterior end of metasoma, lateral aspect; 52, hind coxa, lateral aspect.



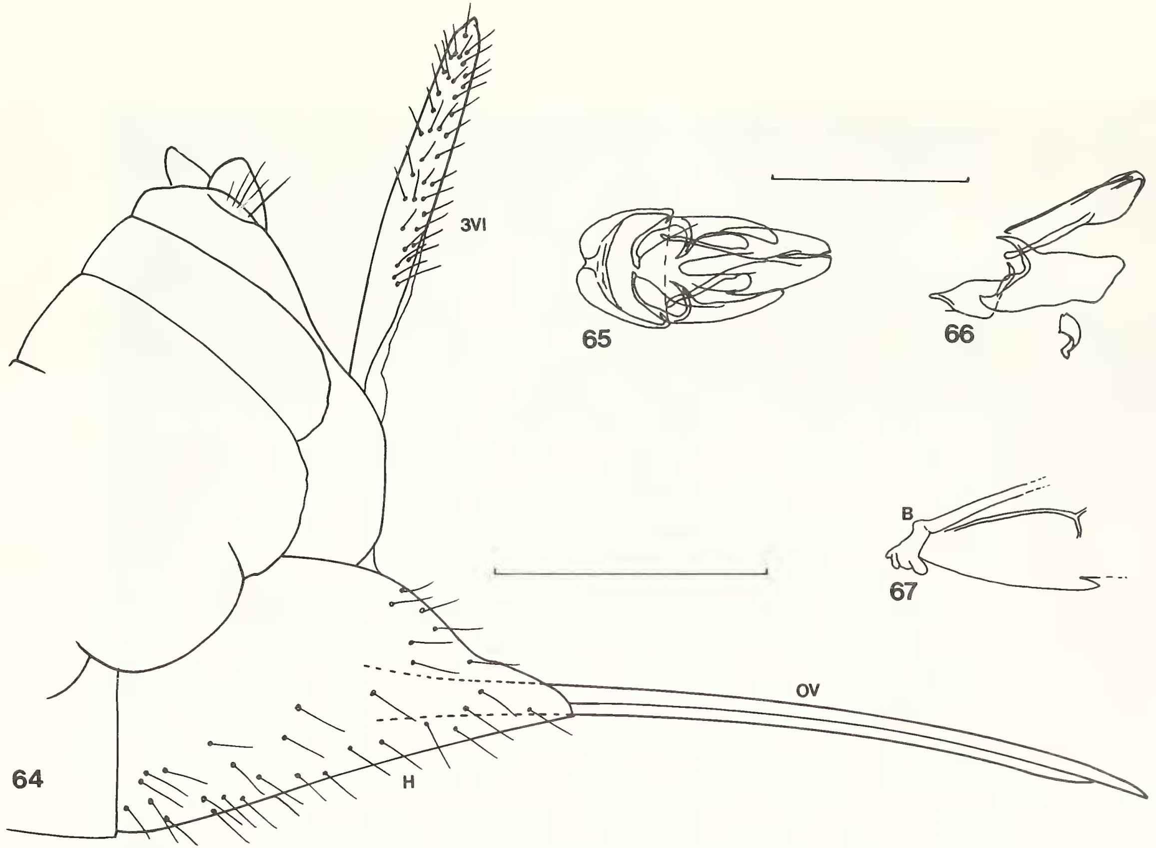
Figs. 53-54. Line drawings of *Sathon laevidorsum* female. Scale bar = 0.5mm: 53, apex of metasoma, lateral aspect (H = hypopygium; 3VL = third valvula; OV = ovipositor); 54, anterior edge of right hind wing, anteroventral aspect (B = bulb on SC+R).



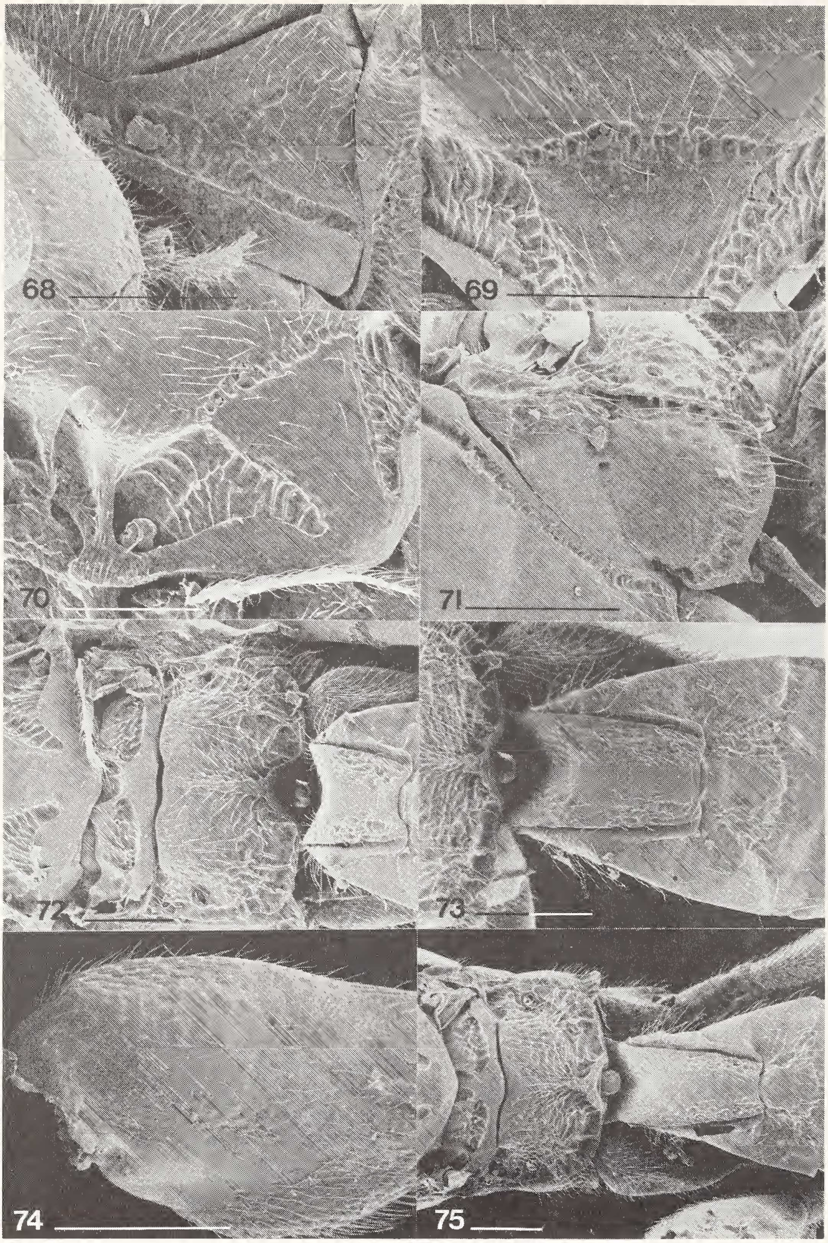
Figs. 55–60. S.E.M. photographs of *Sathon aggeris* female. Scale bars = 0.5mm: 55, metanotum and propodeum, dorsal aspect; 56, anterior end of metasoma, dorsal aspect; 57, anterior end of metasoma, lateral aspect (T1 = first tergum of metasoma); 58, hind coxa, lateral aspect; 59, metanotum and propodeum of male, dorsal aspect; 60, anterior end of metasoma of male, dorsal aspect;



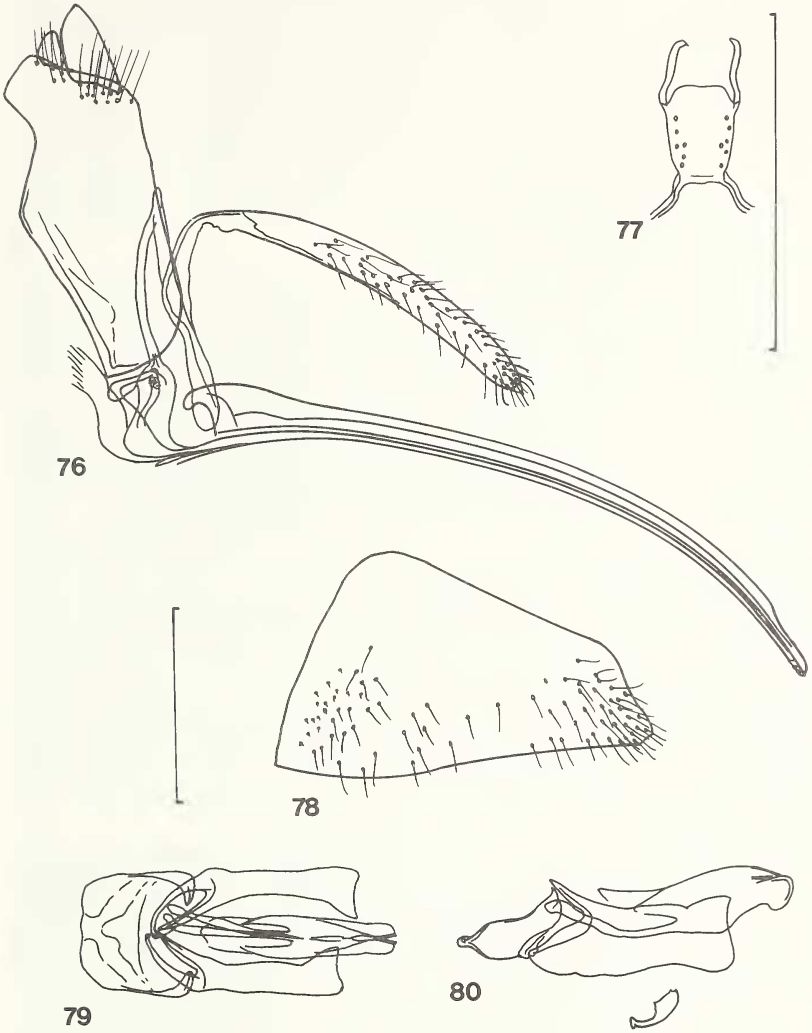
Figs. 61–63. Line drawings of *Sathon aggeris* female from S.E.M. photographs. Scale bars = 0.2mm. Setae omitted except on pronotal disc, fig. 61: 61, pronotum, lateral aspect; 62, prescutellar furrow, dorsal aspect; 63, scutellum, dorsolateral aspect.



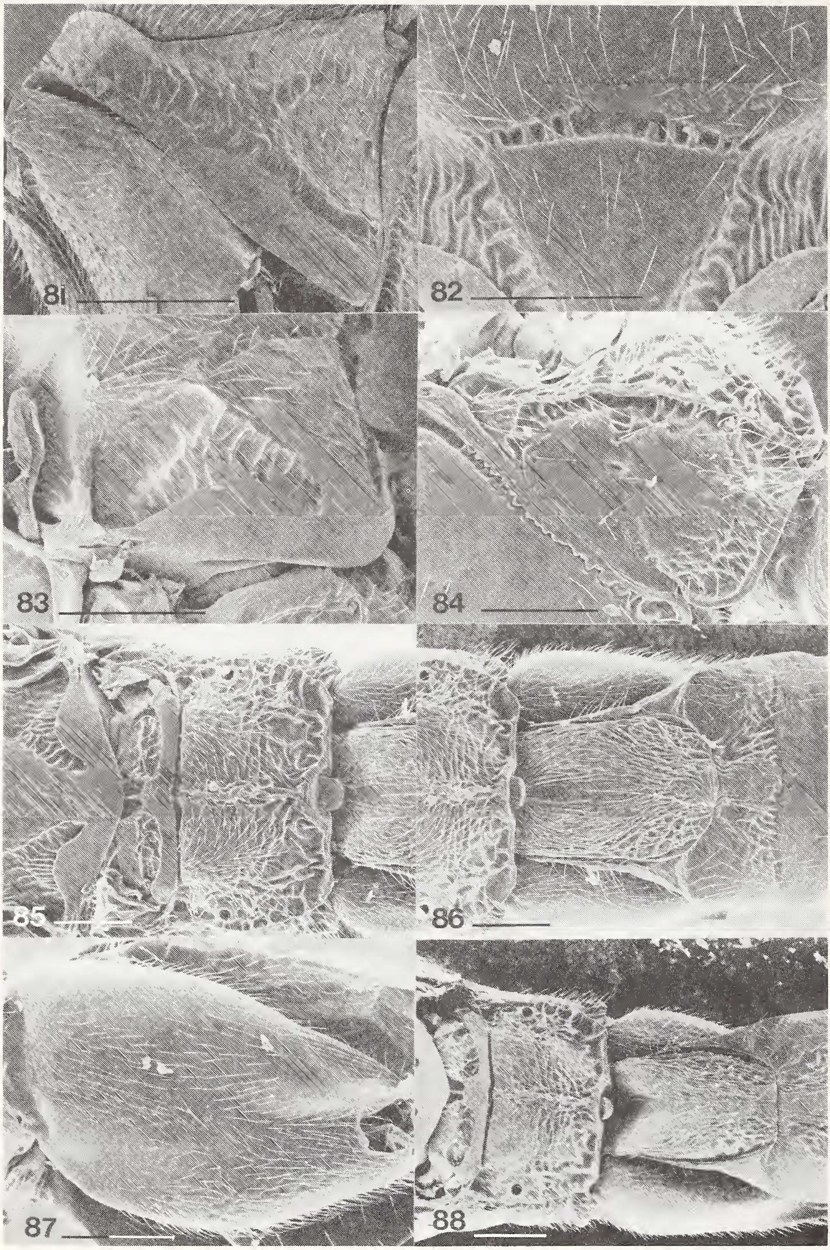
Figs. 64-67. Line drawings of *Sathon aggeris* male and female. Scale bars = 0.5mm: 64, apex of metasoma, lateral aspect (H = hypopygium; 3VL = third valvula; OV = ovipositor); 65, male genital capsule, dorsal aspect, volsellae removed; 66, male genital capsule, lateral aspect, volsellae except digitus removed; 67, anterior edge of right hind wing, anteroventral aspect (B = bulb on SC+R).



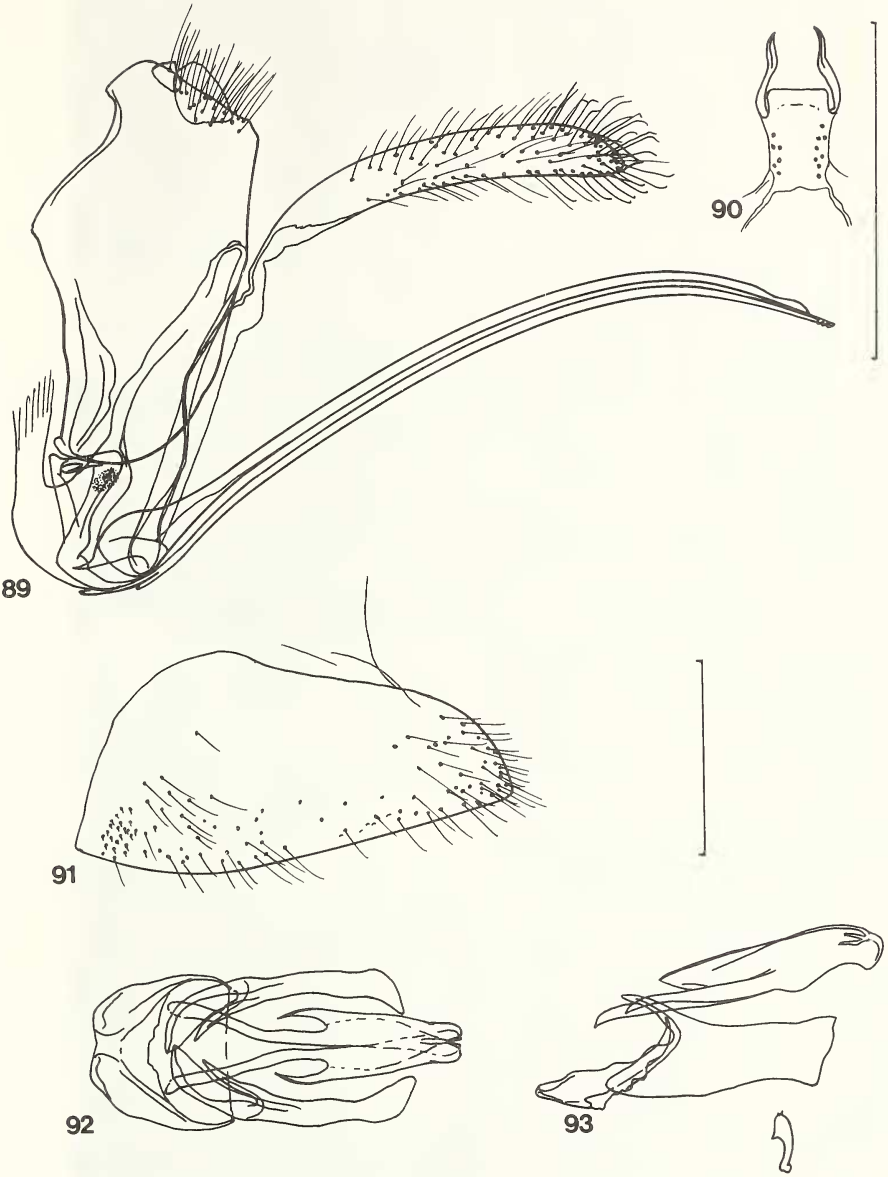
Figs. 68–75. S.E.M. photographs of *Sathon masoni* female. Scale bars = 0.2mm: 68, pronotum, lateral aspect; 69, prescutellar furrow, dorsal aspect; 70, scutellum, dorsolateral aspect; 71, metapleuron, lateral aspect; 72, metanotum and propodeum, dorsal aspect; 73, anterior end of metasoma, dorsal aspect; 74, hind coxa, lateral aspect; 75, meso- and metasoma of male, dorsal aspect.



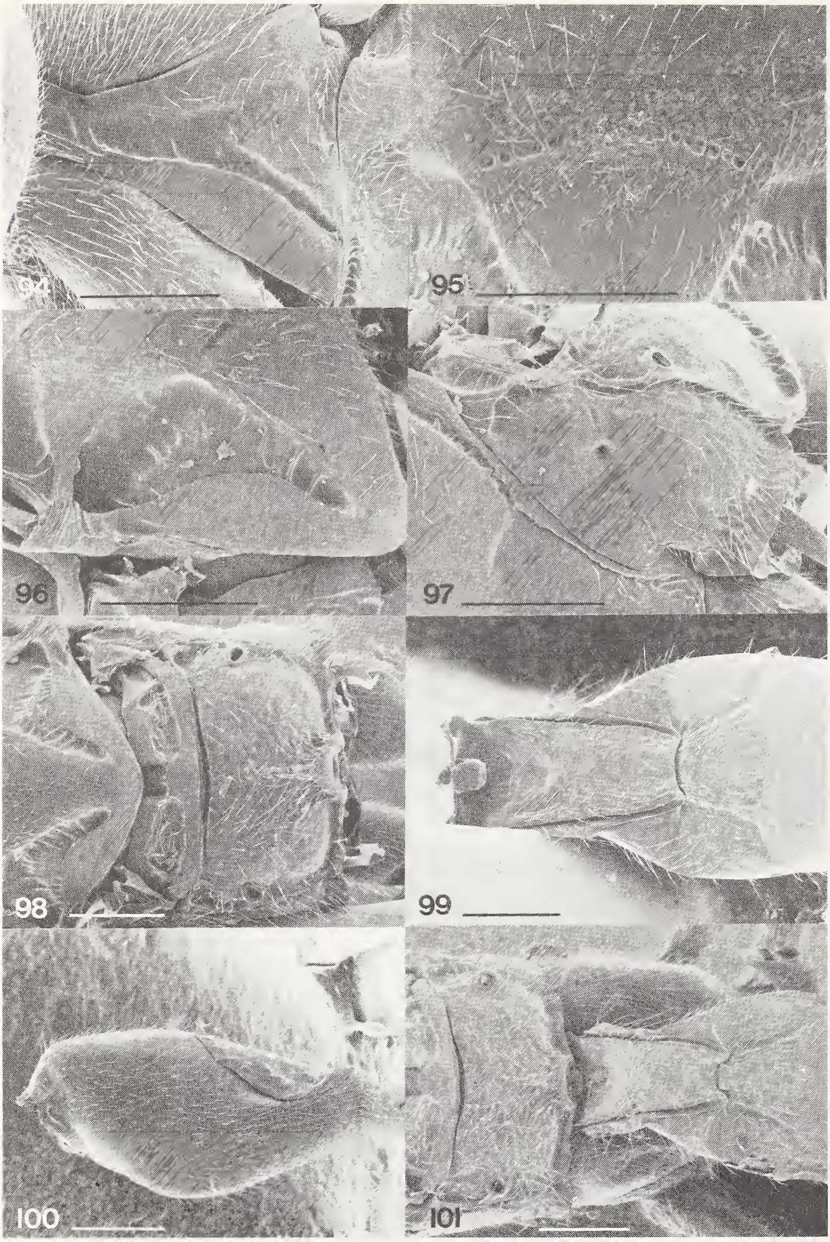
Figs. 76–80. Line drawings of *Sathon masoni* male and female. Scale bars = 0.5mm: 76, female genitalia, lateral aspect; 77, oral plate of female, anterior aspect; 78, hypopygium, lateral aspect; 79, male genital capsule, dorsal aspect, volsellae removed; 80, male genital capsule, lateral aspect, volsellae except digitus removed.



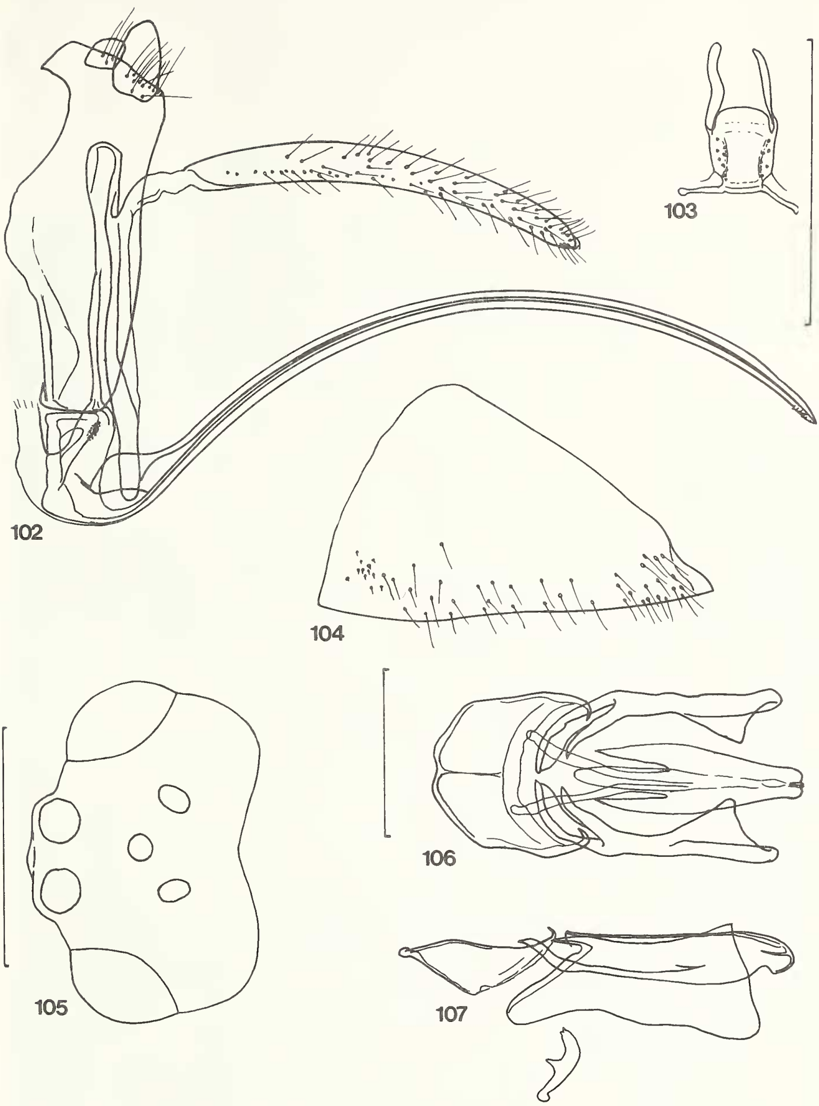
Figs. 81–88. S.E.M. photographs of *Sathon cinctiformis* female. Scale bars = 0.2mm: 81, pronotum, lateral aspect; 82, prescutellar furrow, dorsal aspect; 83, scutellum, dorsolateral aspect; 84, metapleuron, lateral aspect; 85, metanotum and propodeum, dorsal aspect; 86, anterior end of metasoma, dorsal aspect; 87, hind coxa, lateral aspect. 88, meso- and metasoma of male, dorsal aspect.



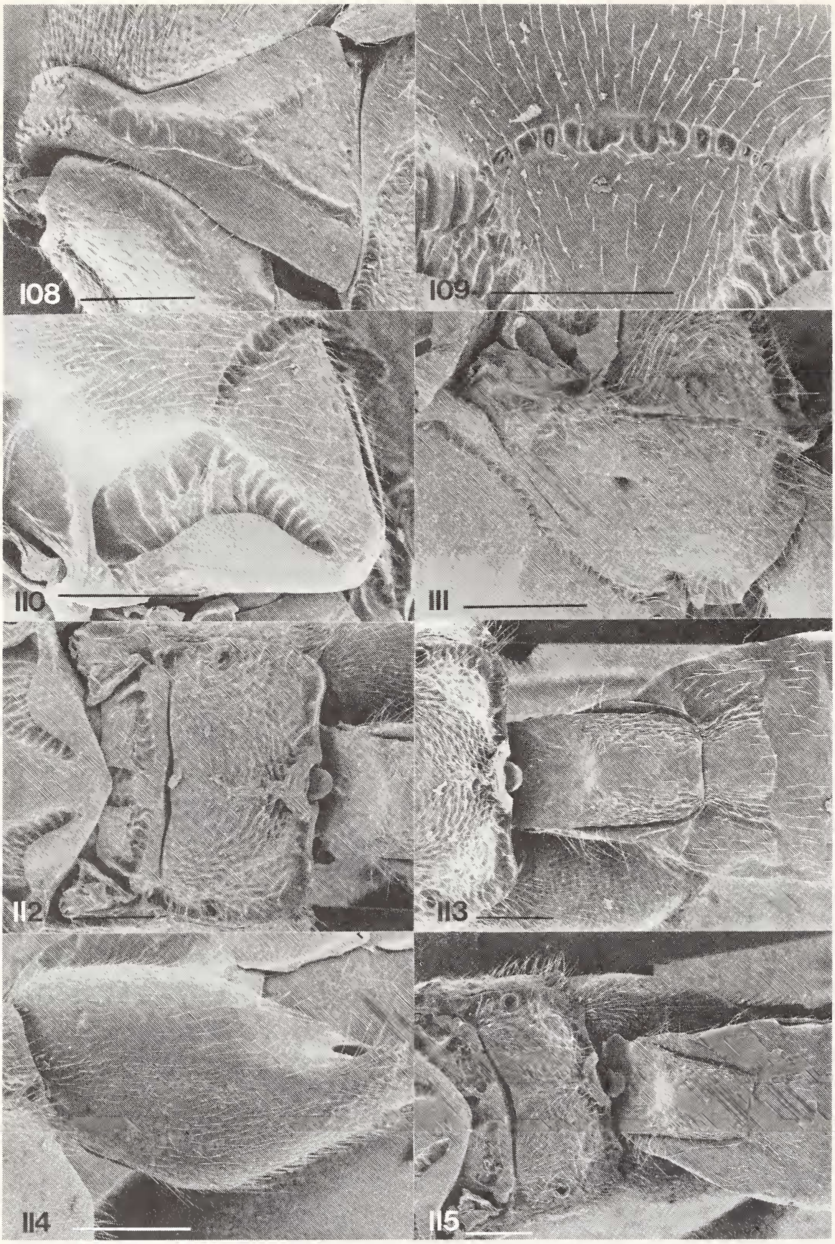
Figs. 89–93. Line drawings of *Sathon cinctiformis* female and male. Scale bars = 0.5mm: 89, female genitalia, lateral aspect; 90, oral plate of female, anterior aspect; 91, hypopygium, lateral aspect; 92, male genital capsule, dorsal aspect, volsellae removed; 93, male genital capsule, lateral aspect, volsellae except digitus removed.



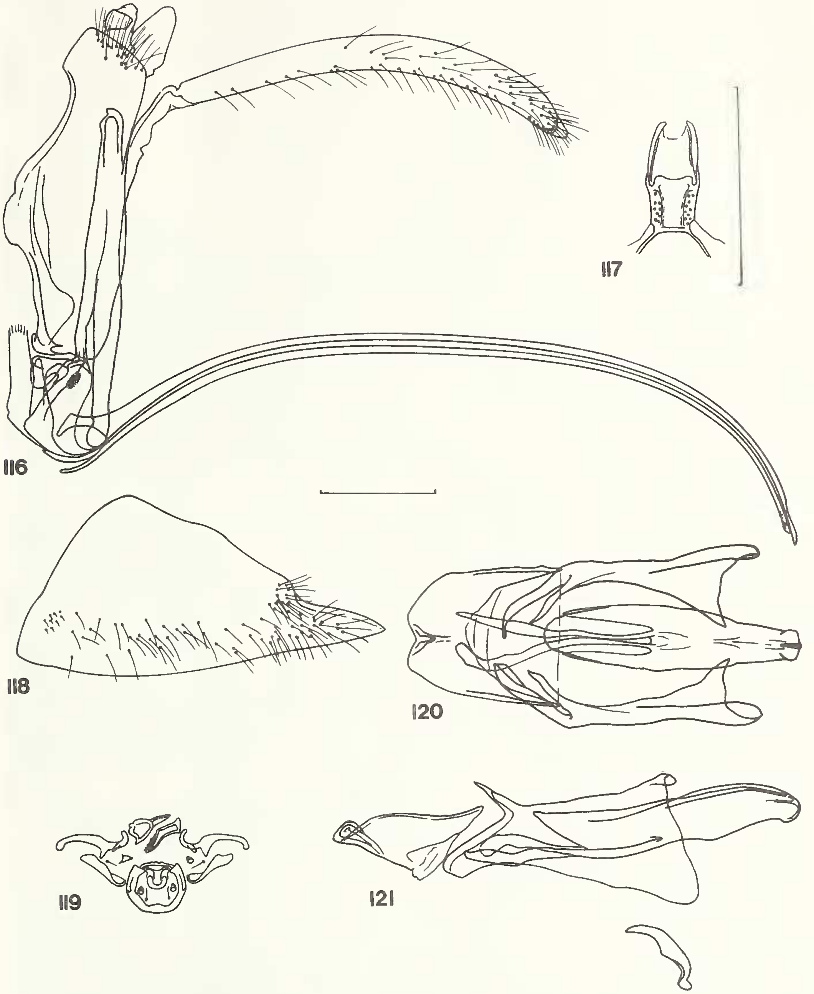
Figs. 94–101. S.E.M. photographs of *Sathon circumflexus* female. Scale bars = 0.2mm: 94, pronotum, lateral aspect; 95, prescutellar furrow, dorsal aspect; 96, scutellum, dorsolateral aspect; 97, metapleuron, lateral aspect; 98, metanotum and propodeum, dorsal aspect; 99, anterior end of metasoma, dorsal aspect; 100, hind coxa, lateral aspect; 101, meso- and metasoma of male, dorsal aspect.



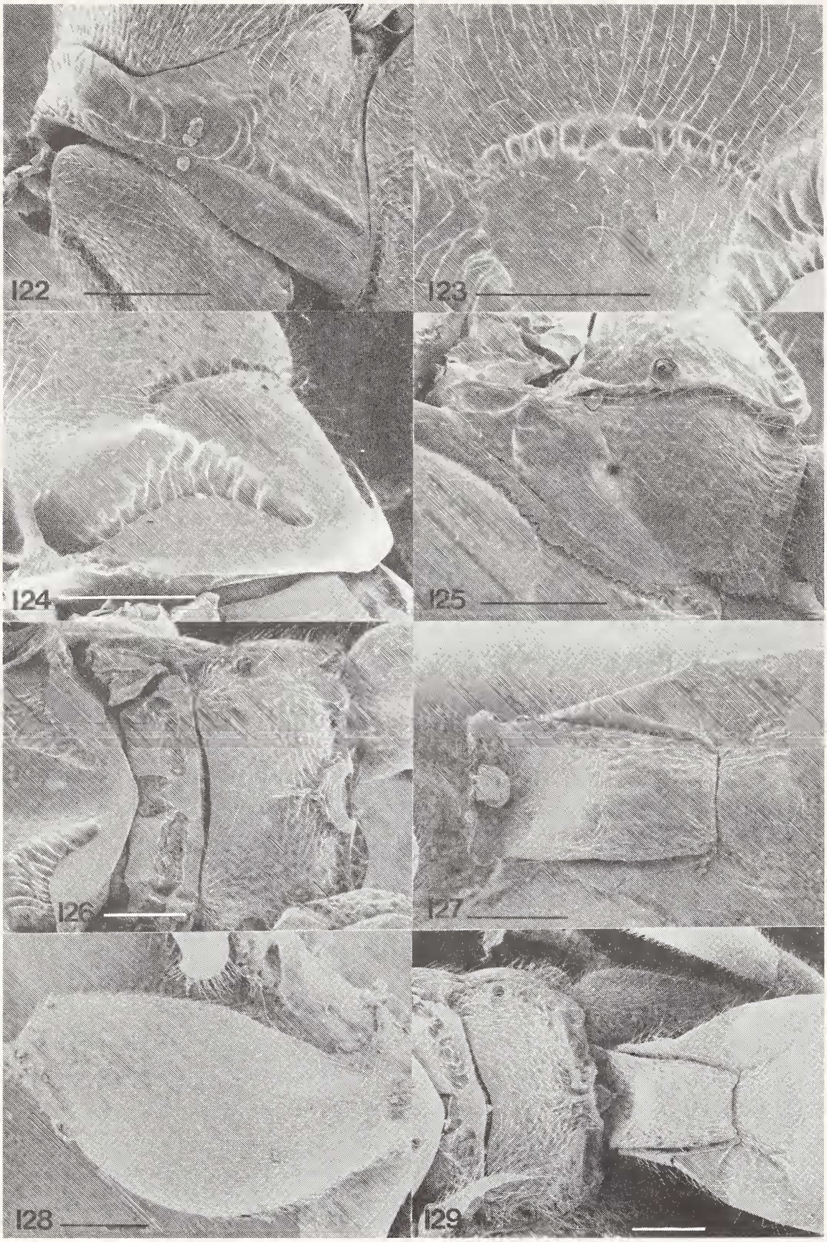
Figs. 102–107. Line drawings of *Sathon circumflexus* female and male. Scale bars = 0.5mm: 102, female genitalia, lateral aspect; 103, oral plate of female, anterior aspect; 104, hypopygium, lateral aspect; 105, head of adult, dorsal aspect; 106, male genital capsule, dorsal aspect, volsellae removed; 107, male genital capsule, lateral aspect, Volsellae except digitus removed.



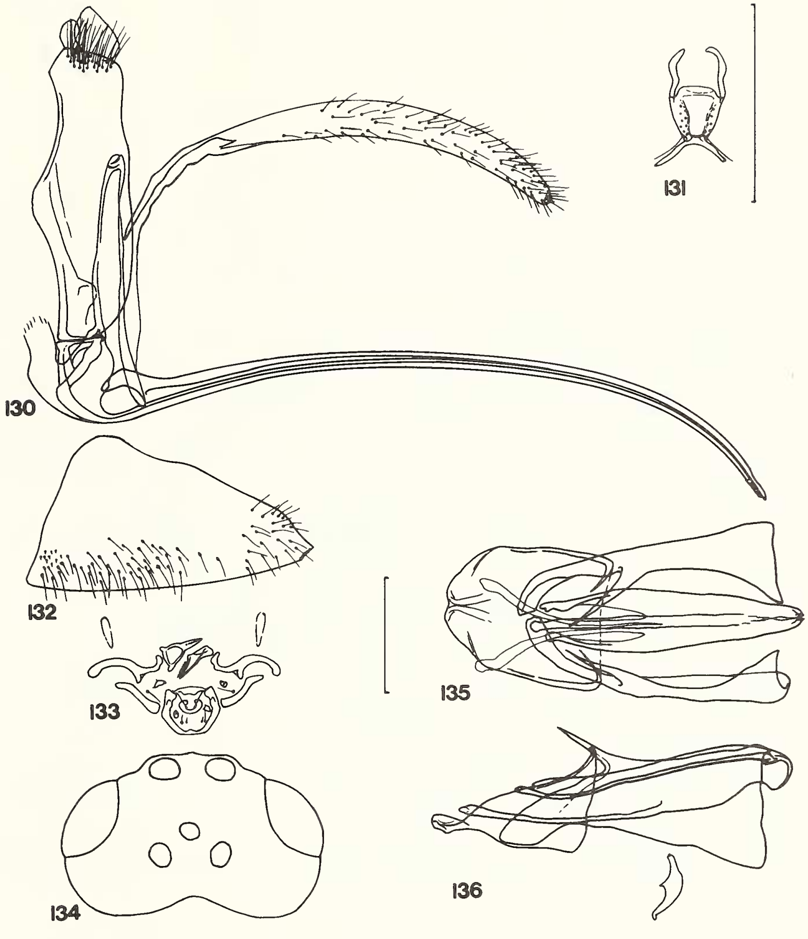
Figs. 108–115. S.E.M. photographs of *Sathon neomexicanus* female. Scale bars = 0.2mm: 108, pronotum, lateral aspect; 109, prescutellar furrow, dorsal aspect; 110, scutellum, dorsolateral aspect; 111, metapleuron, lateral aspect; 112, metanotum and propodeum, dorsal aspect; 113, anterior end of metasoma, dorsal aspect; 114, hind coxa, lateral aspect; 115, meso- and metasoma of male, dorsal aspect.



Figs. 116–121. Line drawings of *Sathon neomexicanus* female and male. Scale bars = 0.5mm: 116, female genitalia, lateral aspect; 117, oral plate of female, anterior aspect; 118, hypopygium, lateral aspect; 119, head capsule of larva, anterior aspect; 120, male genital capsule, dorsal aspect (volsellae removed); 121, male genital capsule, lateral aspect (volsellae except digitus removed).



Figs. 122–129. S.E.M. photographs of *Sathon falcatus* female. Scale bars = 0.2mm: 122, pronotum, lateral aspect; 123, prescutellar furrow, dorsal aspect; 124, scutellum, dorsolateral aspect; 125, metapleuron, lateral aspect; 126, metanotum and propodeum, dorsal aspect; 127, anterior end of metasoma, dorsal aspect; 128, hind coxa, lateral aspect; 129, meso- and metasoma of male, dorsal aspect.



Figs. 130–136. Line drawings of *Sathon falcatus* female and male. Scale bars = 0.5mm: 130, female genitalia, lateral aspect; 131, oral plate of female, anterior aspect; 132, hypopygium, lateral aspect; 133, head capsule of larva, anterior aspect; 134, head of adult, dorsal aspect; 135, male genital capsule, dorsal aspect, volsellae removed; 136, male genital capsule, lateral aspect, volsellae except digitus removed.

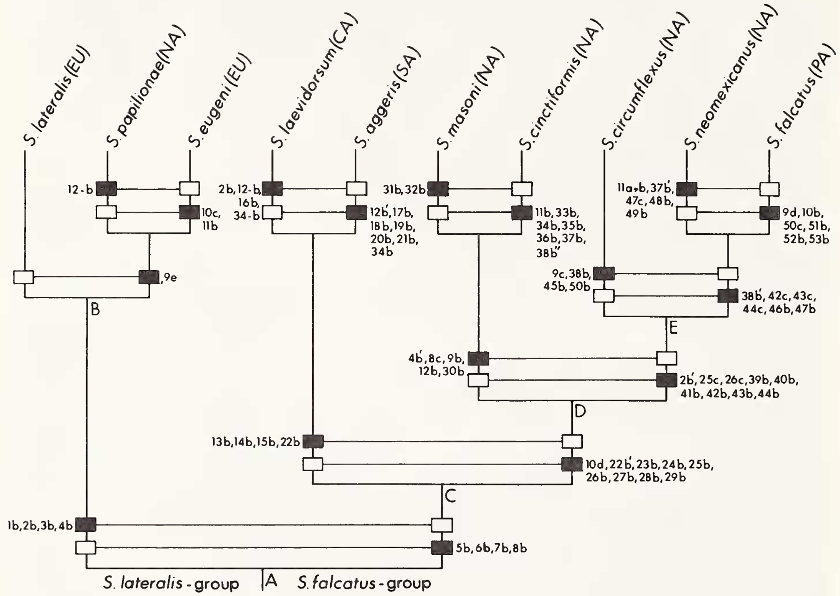


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Fig. 137. Reconstructed phylogeny of *Sathon* species. For explanation of characters and dichotomy coding see text. CA = Central America; EU = Europe; NA = North America PA = Palaearctic; SA = South America.

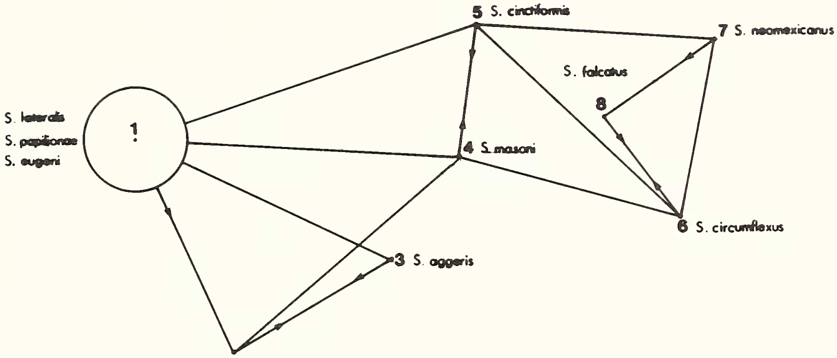

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Fig. 138. Cluster diagram of phenetic analysis of *Sathon* species. Each clusters nearest neighbor indicated by arrow on lines. The distance between *S. Aggeris* and *S. masoni* is greater than indicated.

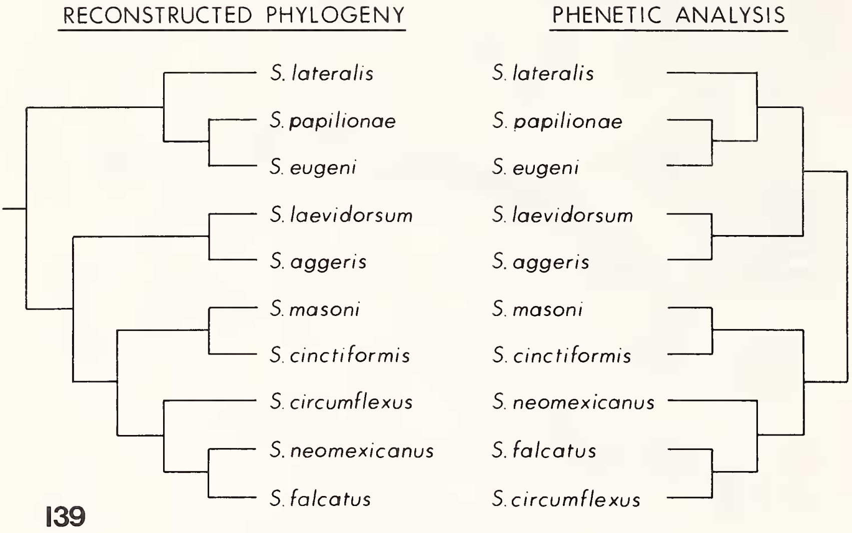

Fig. 139. Comparison of phylogenetic reconstruction and information from phenetic analyses of *Sathon* species. Degree of divergence not indicated.

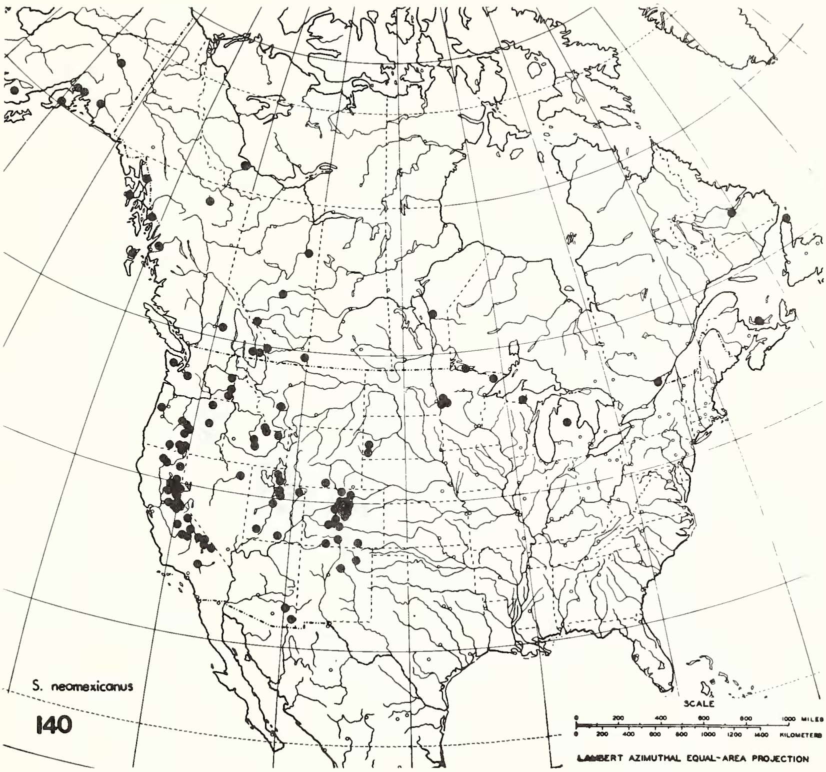

Fig. 140. Geographical distribution of *Sathon neomexicanus*. All dots represent localities from which *S. neomexicanus* specimens were examined in this study.

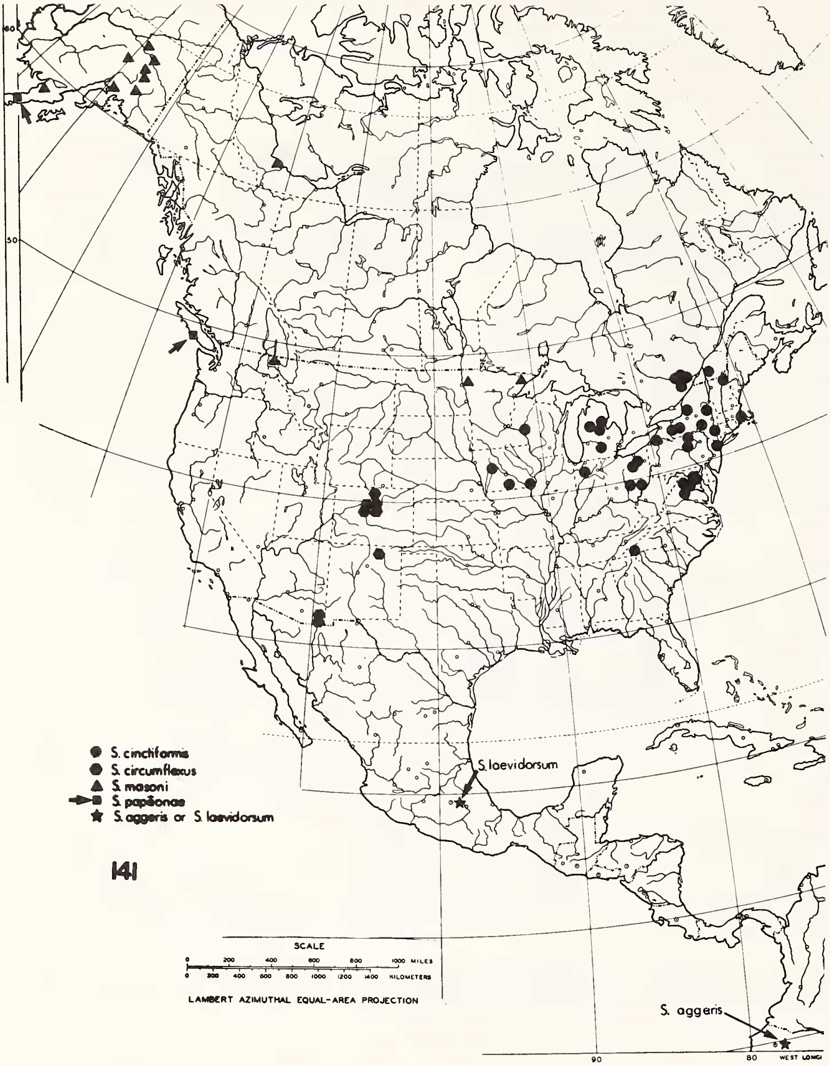

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Fig. 141. Geographical distribution of American species of *Sathon* exclusive of *S. neomexicanus*. All dots represent localities from which specimens were examined in this study.

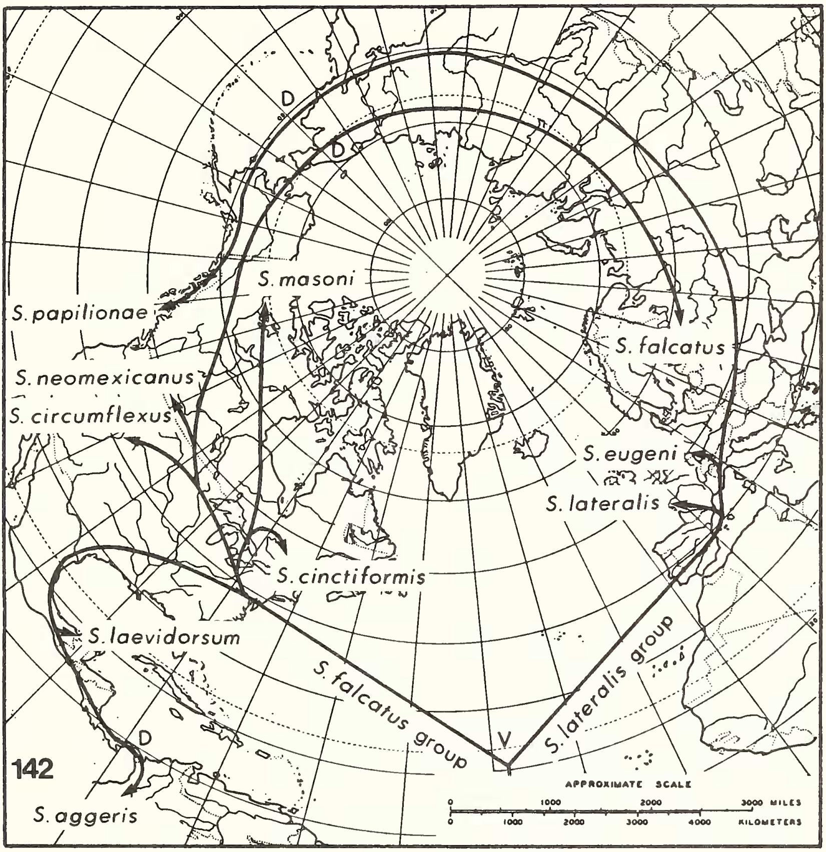

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Fig. 142. Geographical history of *Sathon* species, based on known distributions and reconstructed phylogenetic relationships. On polar projection. Arrows do not indicate direction of dispersal unless specifically indicated. D = probable dispersal route. V = probable vicariance event.

APPENDIX 1. TABLE OF RATIOS

Table 6. Non-coded, morphometric characters in *Sathon* species.

For discussion of characters see text and see figs. 1 to 8 for measurement methods and structure abbreviations (abbreviations not given are PF = penultimate flagellomere and PFT = penultimate fore tarsomere). Columns are arranged with mean, range and standard deviation for each species. Sample sizes are listed after each species abbreviation. lat = *S. lateralis*, pap = *S. papilionae*, eug = *S. eugeni*, lev = *S. laevidorsum*, agg = *S. aggeris*, mas = *S. masoni*, cin = *S. cinctiformis*, cir = *S. circumflexus*, neo = *S. neomexicanus*, fal = *S. falcatus*.

Chars.	HW/HL	Clypeus W/H	pol/ool	pol/lol	lod/aod	lol/aod	PF W/L	PFT L/W	HW/HCL	SL/ SW	2r/1Rs	1Rs+M/ 1M	1Cu1/ m-cu
lat(6)	1.71	2.76	0.85	2.68	1.12	0.59	0.78	1.31	0.96	2.50	1.10	1.04	1.03
	1.54-1.88	2.55-2.91	0.76-0.94	2.50-3.00	1.05-1.22	0.56-0.67	0.67-0.90	1.13-1.50	0.88-1.04	–	1.00-1.30	1.02-1.10	0.96-1.08
	0.12	0.13	0.06	0.19	0.06	0.04	0.08	0.16	0.96	–	0.12	0.14	0.04
pap(2)	1.68	2.63	0.96	2.91	1.16	0.67	0.50	1.42	1.14	2.50	0.98	1.05	0.89
	1.63-1.73	2.50-2.73	0.76-1.13	2.57-3.25	1.13-1.18	0.47-0.86	–	1.33-1.50	1.13-1.15	–	0.96-1.00	1.02-1.08	0.88-0.90
	-	–	-	–	-	–	-	–	-	–	-	–	
eug(6)	1.82	2.91	0.74	2.37	1.10	0.64	0.62	1.41	0.99	2.50	1.04	1.04	0.92
	1.72-2.00	2.73-3.09	0.69-0.75	2.14-2.50	1.00-1.22	0.56-0.78	0.57-0.77	1.14-1.50	0.91-1.02	–	0.93-1.15	0.97-1.26	0.84-0.98
	0.11	0.13	0.06	0.17	0.07	0.08	0.09	0.13	0.06	–	0.08	0.11	0.05

(continued on next page)

Table 6 (continued)

Chars.	HW/HL	Clypeus W/H	pol/ool	pol/lol	lod/aod	lol/aod	PF W/L	PFT L/W	HW/HCL	SL/ SW	2r/1Rs	1Rs+M/ 1M	1Cu1/ m-cu
lev(1)	1.67	3.00	0.65	2.60	1.14	0.71	0.67	1.33	1.00	2.60	1.16	1.05	1.00
	-	–	-	–	-	–	-	–	-	–	-	–	
	-	–	-	–	-	–	-	–	-	–	-	–	
Char.	HW/HL	Clypeus W/H	pol/ool	pol/lol	lod/aod	lol/aod	PF W/L	PFT L/W	HW/HCL	SL/ SW	2r/1Rs	1Rs+M/ 1M	1Cu1/ m-cu
agg(1)	1.70	3.90	0.69	2.67	1.13	0.75	0.66	1.83	0.90	3.00	1.83	0.93	1.00
	-	–	-	–	-	–	-	–	-	–	-	–	
	-	–	-	–	-	–	-	–	-	–	-	–	
mas(16)	1.72	2.95	0.81	2.13	1.10	1.10	0.87	1.28	1.21	2.50	0.77	0.97	0.96
	1.62-1.81	2.67-3.33	0.62-0.95	1.75-2.43	1.00-1.25	0.93-1.33	0.78-1.00	1.17-1.33	1.10-1.49	–	0.58-0.91	0.92-1.04	0.83-1.10
	0.05	0.22	0.09	0.19	0.10	0.12	0.08	0.08	0.09	–	0.08	0.03	0.07
cin(15)	1.68	3.04	0.78	2.25	1.15	0.84	0.69	1.10	1.13	2.80	0.77	0.96	0.96
	1.57-1.78	2.80-3.30	0.67-0.89	1.89-2.67	1.00-1.43	0.67-1.00	0.62-0.82	1.00-1.28	0.99-1.53	–	0.57-0.95	0.92-1.00	0.74-1.11
	0.07	0.17	0.06	0.23	0.11	0.11	0.06	0.10	0.12	–	0.10	0.02	0.10

(continued on next page)

Table 6 (continued)

Chars.	HW/HL	Clypeus W/H	pol/ool	pol/lol	lod/aod	lol/aod	PF W/L	PFT L/W	HW/HCL	SL/ SW	2r/1Rs	1Rs+M/ 1M	1Cu1/ m-cu
cir(15)	1.83	3.00	0.93	2.40	0.97	0.79	0.67	1.23	1.17	2.00	1.03	1.10	1.16
	1.67-1.98	2.58-3.33	0.80-1.00	2.00-2.83	0.89-1.05	0.67-0.89 0.57-0.75	1.14-1.38	1.10-1.26	–	0.87-1.24	1.06-1.17	0.95-1.39	
	0.07	0.19	0.06	0.21	0.06	0.08	0.05	0.09	0.05	–	0.09	0.03	0.10
neo(35)	1.87	3.00	0.92	2.22	1.07	0.84	0.63	1.23	1.11	2.40	0.85	1.06	1.00
	1.66-2.08	2.54-3.50	0.81-1.05	1.88-2.67	0.91-1.25	0.60-1.00	0.53-0.69	1.00-1.43	0.97-1.28	–	0.57-1.18	0.98-1.13	0.82-1.15
	0.09	0.24	0.07	0.17	0.07	0.10	0.04	0.18	0.06	–	0.10	0.04	0.11
fal(25)	1.89	3.06	0.99	2.27	1.14	0.83	0.79	1.06	1.06	2.50	0.98	1.12	1.13
	1.75-2.03	2.75-3.30	0.88-1.12	2.11-2.50	1.00-1.33	0.73-0.90	0.69-0.91	1.00-1.13	1.00-1.14	–	0.78-1.13	1.02-1.19	0.88-1.35
	0.07	0.13	0.06	0.13	0.07	0.06	0.06	0.06	0.03	–	0.09	0.04	0.10

APPENDIX 2. LOCALITY DATA: MATERIAL EXAMINED FOR PREVIOUSLY DESCRIBED SPECIES

(Type material not included)

S. eugeni

Germany: Female, Germany '65 Mainz Sept. 10 A.W. Steffan (CNC). **Italy**: Female, Campi, Riva s. Garda 1400m. E/7.7.66 Hbth (LAZ). **Holland**: Female, Nederlands Oostbroek im Den Bilt coll. 25.V.1979 R. v. Oostenbragge. ex leafroller on Urtica dioica d. (RNH). **Sweden**: Female, Skåne, Sweden VII '69 Trap 4 Bo Svensson (HT). Female, Sweden Vmld. Ekshärad July 23 1960 W.R.M. Mason (CNC). 2 females, Sweden. Sk. Skäralid 3.vii.1938 D.M.S.P. & J.F.P., B.M. 1938–414 (BMNH). **Bulgaria**: 2 females, BULGARIA Rhodopi Chrabrino 15.V.1978, 9.X.1977 (DJMW).

S. lateralis

England: 2 males, 2 females, Torquay, Devon ENGLAND 19–vi–1960 J.R. Vockeroth (CNC). Male, female, ENGLAND East Sussex Staplecross 15–19.ix.38 RF 139. D.S. Wilkinson & R.L.E. Ford. Swept off nettle where Simaethis fabriciana abundant (BMNH). **Germany**: Female, Gessernhausen Brennessel leg. Schwenke 14./E.5.69 Z.59 (LAZ). **Irelend**: 6 males, 4 females, Finglas, Ireland vi.44 B.P. Beirne Ex Simaethis fabriciana (CNC). 2 females, Ballybrack, Ire vi.41 B.P. Beirne Ex Simaethis fabricians (CNC). **Holland**: Male, NEDERLAND Waarder (Z.H.) Oosteinde 34 2–3.X.1971 C van Achterberg. Alnus–Salix–forest. on peat in cult. area, Townes–trap (RNH). Male, NEDERLAND Waarder (Z.H.) Oosteinde 1–5.VII.1971 C. van Achterberg (RNH). Male, 5 females, NEDERLAND (Z.H.) Waarder: at 0.33 in Malaise Trap 16–31 Sept. 1973 (DJMW). Male, female, Nederlands, Oostbroek 1250 im. Den Bilt. coll. 1.VI.1979 R.v. Oostenbragge. ex leafroller on Urtica dioica d. (RNH).

S. cinctiformis

Canada. Ontario: 2 males, female, Ottawa, Ont. 19–VII–1939, 28–VI–1940, O. Peck (CNC). Female, Ottawa Can P310 Type Apanteles cinctus Prov. (USNM). Female, Ottawa, Ont. 9–VII 1946 G.S. Walley Dow's Swamp (CNC). Female, Ottawa, Ont. 21–VII 1950 W.R.M. Mason (CNC). **Quebec**: 2 females, Gracefield, Que. 15–VI.1937 O. Peck (CNC). Female, Wakefield, Que. 9.VII 1946 G.E. Shewell (CNC). Male, Brome, Que. 12–VI 1936 G.S. Walley (CNC). **United States. Indiana**: 2 male, female, Lafayette Ind May 1918 JM Aldrich coll (USNM). **Iowa**: 2 male, 2 female, County #76 IOWA May 26 1934 Knutson (USNM). Male, County #59 IOWA May 1934 Jolley (USNM). Female, Mt Pleasant Ia May 26 1934 Card (USNM). **Maryland**: Female, Takoma Park, VI.14, 1942 Md. H. & M. Townes (HT). Female, Cabin John Md. July 1916 RM Fouts Collector (USNM). Female, Patuxent Ref Bowie, Md. 28–V 1944 RT Mitchell Collector (CNC). **Michigan**: 2 male, female, Isabella Co. Mich. 6–7–58 R. & K. Dreisbach (USNM). Female, Gladwin Co. Mich. 6–14–58 R. & K. Dreisbach (USNM). Female, Lake Co. Mich. 7–7–57 R. & K. Dreisbach (USNM). 4 females, Midland Co. Mich. VI.10.41, VII.7.54, 7–18–40, 6–30–52, R.R. Dreisbach (USNM). Female, Ag. Coll. Mich 7–12.9–336 Collection C.F. Baker (USNM). Female, AgrCollege Mich 336 (USNM). **New Jersey**: Female, Summit N.J. 5.26 1925 F.M. Schott (USNM). **New York**: Male, Oswego, N.Y. 11 June, 1897 (USNM). Male, female, Mud Creek, Tompk Co. N.Y. 17–20 June '04 (USNM). 2 male, female, Ithaca, N.Y. V.31, 1936, VI.6, 1935, H.K. Townes (HT).Female, Bemus Pt., N.Y. Jul. 16 1937 H.K. Townes (HT). Female, Oneoata NY June 30 1935 H.K. Townes (HT). Female, Shokan, N.Y. Jul. 11 1936 H.K. Townes (HT). Female, Canajoharie, N.Y. Jul. 1, 1934 H.K. Townes (HT). **North Carolina**: Female, Franklin, N.C. 2000' 8.11 1957 J.R. Vockeroth (CNC). **Ohio**: 3 females, Barberton Ohio 6–22–36 L.J. Lipovsky (UKL). 2 females, Summit Co., Ohio 6–19 1937 Louis J. Lipovsky (UKL). Female, Conservation Cage Jerusalem Ohio In3 Ser33–1 LG Jones Coll 6/10/33 (USNM). Female, Ohio F.D. DeGant Collector (USNM). Female, Lick. Co. V–'26 O. C.H. Kennedy Collector, C.H. Kennedy Collection (USNM). **Pennsylvania**: Female, Wilawana, Pa. 6–9 1939 R.H. Crandall (USNM). Female, Ralston Lycoming Co. Pa. 8.VI.1962 J.R. Vockeroth (CNC). **Rhode Island**: Male, 8 females, Westerly, R.I. VI.9, VI.10, VI.21, VII.7, 1936 M. Chapman (HT). Female, Westerly R.I. VI.12.37 H.K. Townes M. Chapman (HT). **Vermont**: Female, Lake Willoughby, Vt. Alt. 1400ft. June 17–29, 1945 C.P. Alexander (HT). **Virginia**: 3 males, 3 females, Sweeping sedges & grasses Vienna Va J.C. Bridwell coll V–19–35 (USNM).Female, Va July 4.85 (USNM). Female, Great Falls Va H.H. Smith coll (USNM). Female, Ch. Bridge XI.19 Va SA Rohwer coll (USNM). **Wisconsin**: Female, Polk Co. Wis. July. Baker. Collection CF

Baker (USNM).

S. falcatus

Austria: Male, 14 females, AUSTRIA Tirol Aschbach 1400m 16, 20–VIII 1975 C.J. Zwakhals (RNH). 2 females, AUSTRIA, Raxalpe 1500m Aug.20, 1960 W.R.M. Mason (CNC). Female, Zwieselstein TIROL 1400m. 24.VIII.1953 J.R. Vockeroth (CNC). **England**: Female, ENGLAND. HT. Bricket Wood. 5.v.1950 R.B. Benson B.M. 1950–286 (BMNH). Male, 5 females, ENGLAND North Devon Romansleigh R.L.E. Ford Swept 26.vi.38 (CNC, USNM). 5 females, Ditchling Common 1.VIII.1951. Sx. G.E. Shewell ENGLAND (CNC). 5 males, 3 females, ENGLAND Birmingham spun 16.vii.55 em. 20.vii.55 [with two cocoon masses] (BMNH). **France**: Male, 2 females, Malaucène Mt. Ventoux 1400m. Nardion pasture 23.VII.1973 FRANCE Dept. Vaucluse M.J. Gijswijt (RNH). **Germany**: 5 females, Scheffau, Bayern GERMANY, 800m. 25–VII–1958 David Townes (CNC). Female, D, By, Starnberg Kerschlach 27.7.74 Haeselb. (LAZ). Female, Wiesen/Spessart 6.8.1961 leg. Haeselbarth (LAZ). 3 females, Schliersee BAVARIA 7–1100m. 28.VII.1958 David Townes (CNC). 2 females, Germany Collection T Pergande 26 (USNM). **Holland**: Female, Holland 28–7–49 Schayk H. Teunissen (RNH). Female, Oploo HT V–5 1972 (RNH). 3 females, NEDERLAND Waarder (Z.H.) Oosteinde 34 3–4, 13–14, 27–28.VII.1971 C. van Achterberg (RNH). **Italy**: 8 males, 20 females, Naturno, Trentino ITALY 500–1000m., 1000m., 14–VII, 15–VII, 18–VII.1958 David Townes (CNC). Female, Unserfrau, 1500m nr. Mont Alto, Trentino, ITALY 18–VII–1958 David Townes (CNC). Male, St. Peter/Ahrntal [=San Pietro], Südtirol 1300m. Cd/31.7.66 Haeselbarth (LAZ). Female, S. Pietre 1200–1400m Funes–[Villnö] prov. Bolzano–Italia 20.vii -9.viii.1968 G. van Rossem (RNH). Female, Selva Nera 1400–2000m Funes–[Villnö] prov. Bolzano–Italia 20.vii–9.viii.1968 G. van Rossem (RNH). **Ireland**: Female, M–IRELAND nr. Rhode (3) Heath, on umbelliferous flowers 11–VIII. 1974 C.v. Achterberg (RNH). **Luxemburg**: Female, LUXEMBURG Diekirch, 20–V/A.W. Steffan '66 (CNC). **Spain**: Female, LA MOLINA 1500m 23–VII–1970 ESPANIA Gerona V.S.v.d. Goot J.A.W. Lucas (RNH). **Sweden**: 20 males, 60 females, SWEDEN, Vmld. Ekshärad July 15, 17, 20, 21, 22, 23, 24, 1960 W.R.M. Mason (CNC). Male, 7 females, SWEDEN, Lpld. Abisko, 400m. July 2, 30, Aug 1, 2, 30, 1960 W.R.M. Mason (CNC). **Switzerland**: Female, CH, GR, Ramosch 165om 4.8.73 Wiesen u.Wald mit Hochstauden Haeselb. (LAZ). **Yugoslavia**: Female, Yougoslavia, Slovenia Swept:16–8–1978 leg. H.V. Vlug stol. 1000m (RNH). **Other**: 6 females, no locality data, 2 det. by O. Schmiedeknecht (USNM).

S. neomexicanus

Canada. Alberta: 5 males, 3 females, Canada Alberta, Livingstone Ranger Stn. 49° 50'N 114° 25'W Malaise, Sweeps 9–31 July, 20 August 1980 D.J. Williams (DJMW, LAZ). Male, 4 females, M. 14 Banff Banff–Jasper Hway 2,3–VIII–1955 R. Coyles (CNC, BMNH). Male, female, McMurray, Alta. 30–VIII–53 G.E. Ball (CNC). Female, Elkwater Lk. Alta. 21–VII–1956 O. Peck (CNC). Female, O. Peck Edmonton, Alta. 13–5–1930 (CNC). Female, Dom. Range Sta. Manyberries, Alta 24.VII.1951 D.F. Hardwick (CNC). **British Columbia**: 3 males, Racing Riv., B.C. 2400ft. VII.25.73 H.&M. Townes (HT). 4 females, Shore, Shuswap L Salmon Arm B.C. 13–VII–49 H.B. Leech Collector (CAS). 3 females, Juskatla, B.C. Q.C. [Queen Charlotte] Islands 9–VIII–1957 E.E. MacDougall (CNC). Female, Lizard Cr. Fernie B.C. 7–VII–1949 Hugh B. Leech (CAS). Female, Kaslo BC 16.9 [or 7?] AN Caudell Collector (USNM). Female, Terrace, B.C. 23.VII–1960 W.R. Richards (CNC). **Prince Edward Island**: Male, Dalvay House Can. Nat. Park P.E.I. 20.Viii–1940 G.S. Walley (CNC). **Northwest Territories**: 3 females, Fort Simpson N.W.T. 15, 17, 19.VIII.1950 D.P. Whillans (CNC). **Newfoundland**: 3 females, Calvert Nfld. 16–VII–1958 Ray F. Morris (CNC) 3 males, 5 females, Goose Bay, Labr. 5, 10, 23, 25, 26.VIII.1948 W.E. Beckel (CNC). Female, Raleigh, Nfld. VIII.4.1975 H.&M. Townes (HT). **Ontario**: Female, Bells Corners Ont. 7–VII 1943 G.S. Walley (CNC). Female, One Sided Lake, ONT. July 31–1960 S.M. Clark (CNC). **Manitoba**: Male, 2 females, Berens River, Man 9–vii–1938 W.J. Brown (CNC). **United States. Alaska**: Female, King Salmon, Naknek R. Alaska 8–VIII–1952 J.B. Hartley (CNC). Female, Seward, Alaska 10–VII–1951 W.J. Brown (CNC). Male, ALASKA: Sitka 0–100m. VII–1970 Collected by N.L.H. Krauss (USNM). Female, Junaeu, Alaska 6 VIII 1958 Wot Coll. (HT). Male, Matanuska Alaska VII–18–44 J Chamberlin 44–27645 Trap (USNM). Female, Chitna Alaska 7 Aug 1956 R.H. Washburn (USNM). Female, Wrangell, ALASKA 1–5.VIII.1951 J.R. McGilllis (CNC). Female, Big Delta Alaska 14.VII 1951 J.R. McGillis (CNC). Female, Eagle Riv., SE Alaska 2 VIII 1958 Wot Coll. (HT). **Arizona**: 2 females, ARIZ. Graham Co. Hospital Flat

Pinaleno Mts. Alt. 8950' 2.VIII.1965 Hugh B. Leech (CAS). Female, ARIZONA: Cochise Co. Southwestern Res. Sta., 5mi W. Portal 24–IX–1966 5400' P.H. Arnaud, Jr. (CAS). **California**: Female, Graeagle Calif. VI.16 1949 E. Schlinger (HT). Female, Lee Vining, Cal. June 22 1948 HMG&D Townes (HT). Male, 3 females, Sagehen Creek Nevada Co., Cal. VII.10.1974 R.M. Bohart (HT). 7 males, 5 females, Sagehen Creek nr. Hobart Mills Nevada Co. Cal. VII–8, 15–1964 (UCD). Female, Sagehen Cr. Nevada Co Calif VII–19 1972 RM Bohart Colr (UCD). Male, 3 females, Sagehen nr. Hobart Mills Calif VII–21–58 R.H. Goodwin Collector (USNM, UCB). 5 males, 3 females, Sagehen Cr., nr Hobart Mills, Nevada Co, Cal. VII–15, 16, 19–64; ME Irwin Malaise in meadow (USNM). 4 males, 2 females, CALIF: Sierra Co. Sagehen Creek Field Station VIII–6–75 M.E. Buegler/E.I. Schlinger (UCB). 4 females, Cal Nevada Co Sagehen Ck nr. Hobart Mills VII–8–1974 Wharton, Coll (BWC). 3 males, 6 females, Prosser Creek, near Hobart Mills, CALIF. 6300' 13.VII.1961 B.H. Poole (CNC). Male, female, CA: Placer Co. old Donner Pass 2 mi E. Norden 9–IX–1983 7000' J.B. Whitfield collector (JWC). Female, Cal Alpine Co 2mi E. Monitor Pass VII–8–74 Wharton Coll (BWC). 3 females, CALIF: Sisk. Co. 1mi NW Bartle, VII–20–66 P. Rude collector (UCB). 4 males, 4 females, McBride Springs, 4800' Mt. Shasta, Siskiyou Co. Calif., July 22, 1965 (CNC). Female, Cedar Pass, 6000' Warner Mts. 8.VIII.65 Modoc Co., Calif. (CNC). 4 males, 3 females, Fish Camp Cal. July 15 1948 HMG&D Townes (USNM). Female, Walker Pass Cal. VII–13–61 E.I. Schlinger Collector (USNM). Female, Bishop, Calif. VII–28–40 R.H. Beamen (UKL). 2 males, Yosemite Nat. Pk. Calif VIII–1 1940 D.E. Hardy (UKL). 2 males, 2 females, Fallen Leaf, Calif. Eldorado Co. 13.VIII.1961 6500' B.H. Poole (CNC). 3 males, 9 females, Truckee, CALIF. 6000' Tahoe Co. 14.VIII.1961 B.H. Poole (CNC). 2 females, Shaver Lake Fresno Co. Calif VII–8,13–56,68 J.B. Hay flight trap, R.O. Schuster Collector (UCB). Male, Hope Valley Alpine Co. Calif VII–18–48 D. Carter Collector (UCB). Male, female, Lake Forest Lake Tahoe Calif. VII.23.49 E.G. Linsley Collector (UCB, USNM). Female, Leland Mdw. Tuolumne Co. Calif. VIII–5–60 E. Jensen Collector (UCB). Male, Leavitt Mdw. Mono Co., Calif. VIII–11–60 E. Jensen Collector (UCB). Female, Cisco Cal Placer Co VII.28 1934 J.C. Downey collector (UCD). Male, 4mi. W Woodfords Cal. Alpine Co. VI–25–1961 A.S. Menke collector (UCD). Female, Smith Mill Cal. 15 mi s.e. Sierraville VII–4–1960 F.D. Parker Collector (UCD). Female, Wawona, Cal. VII–12–48 H.K. Townes (USNM). Female, Lake Tahoe, Cal. Alt 6225ft. VII–24–1949 E.G. Linsley Collector (UCB). **Colorado**: 3 males, 7 females, Loveland Pass W. slope 9850' 28.VII, 8.VIII.1961 COLO. B.H. Poole (CNC). Female, Alamosa Colo. 1963 D.E. Hahn (HT). Male, 2 females, Morley, Colorado Aug. 25, 1940 H.&M. Townes (HT). 3 males, 3 females, Gould, Colo. VIII.6, 7.1974 H.&M. Townes (HT). Female, nr. Estes Pk. Colo. VIII.14.1948 HMG&D Townes (HT). 5 males, 1Females, Estes Park, COLO. 7500' 20–VII–61 J.R. Stainer, S.M. Clark, W.R.M. Mason (CNC). 4 males, 18 females, Doolittle Ranch 9800' Mt. Evans COLO. 17, 23, 31–VII and 3, 8, 9, 10, 12, 13–VIII '61 J.R. Stainer, S.M. Clark, B.H. Poole, W.R.M. Mason (CNC). Female, West Chicago Creek, Idaho Springs Colo., 11.VIII.1961 9800' J.E.R. Stainer (CNC). 6 females, West Chicago Cr. 9800' Clear Cr. Co., COLO. 11–VIII–1961 B.H.Poole, S.M. Clark (CNC). 3 males, 4 females, Chicago Cr. 8800' Clear Cr. Co. COLO. Aug 2,5 1961 B.H. Poole, W.R.M. Mason (CNC). Female, Glen Haven Colo. VIII.3.1947 P.B.&E.R. Lawson (UKL). 2 females, USA: Colorado: Teller County, Florrisant, Petrified Forest Area 2530m 11–VIII–1973 Paul H. Arnaud, Jr. (CAS). Male, 2 females, State Bridge 7000' nr. Bond, COLO. 24–25–VI–61 B.H. Poole, C.H. Mann (CNC). 2 males, female, Fairplay, COLO. 9800'15 July '61 S.M. Clark, W.R.M. Mason (CNC). 2 males, 19 females, Mt. Vernon Cn. nr. Golden COLO. 31–VII–61 7200'C.H. Mann, W.R.M. Mason (CNC). 6 males, 10 females, 4mi. S.W. Golden, Colo. 7400' 31–VII–1961 S.M. Clark (CNC). Female, Jefferson, COLO. 9400' 14–VII–61 S.M. Clark (CNC). Female, Boulder Colo. 8.VIII 1961 C.H. Mann 5300' (CNC). Male, Nederland, COLO. 8200' 29–VI–61 Collector W.R.M. Mason (CNC). Female, Nederland, Colo. 3mi N. 8500' J.G. Chillcott (CNC). Male, Wondervu, Colo. Boulder Co. 8800' 11.VIII.1961 J.G. Chillcott (CNC). Male, Fall R. RMNP Colo. 8600ft Aug 18 48 Evans & Ball (CNC). 3 females, Idaho Springs, 5mi S.W. Colo. 27.VIII.1961 8000', 8600' C.H. Mann (CNC). Female, Gothic, Colo 9600ft 7–1929 Mary J. Brown (USNM). Male, Boulder Canyon Colo. 8–8–60 7800' R.,K. Dreisbach (USNM). Female, Pagosa Springs Col. Baker Collection CF Baker (USNM). Female, Poudre L. Col. RMNP 1100ft. Aug. 11, 1948 HMG&D Townes (USNM). 10 males, 13 females, Colo 1329 [Steamboat Springs, July], 1361 [Foothills w. of Fort Collins, June], 1547 [Fort Collins. 6–7–95], 1583 [Rustic. 7–11–95], 1584 [Fort Collins. 8–1–95], 2009 [Mooris Ranch, Lar. Co. 7–19–96], 2013 [Forresters Ranch. 8–3–96], 2024 [Spicers North Park. 7–18–96], 2044 [Fort Collins. 7–10–96], 2158 [Grizzley Peak. 7–24–96] Collection CF Baker (USNM). **Idaho**: Male, 3 females, 2 1/2 mi N.W. Kilgore, Clark Co., Ida. VII–15–1956 W.F. Barr Collector (USNM). Female, 2mi N Gilmore, Ida. Lemhi Co. VII–24 1959 H.C. Manis Colector (USNM). Male, 2 mi. E. Leadore Lemhi Co. Ida. VII–12–1956 W.F. Barr Collector (USNM). 2 females, Galena Summit Blaine Co. IDA. 15.VII.61 8600'

B,H, Poole (CNC). Male, 3 females, Galena Summit, nr. Stanley, Ida. VIII.4,5.78 8700' H.&M. Townes (HT). Male, 8 females, nr. Stanley, Ida. Aug 3 1978 H.&M. Townes (HT). **Michigan**: Male, Crystal Falls VII or VIII.69 Mich. H.K. Townes (HT). Male, Female, Crawford Co. Mich. VII–10–59 R. and K. Dreisbach (USNM). **Minnesota**: Female, Gentilly Minn. July 12–14 1935 D.G. Denning (USNM). Female, U.S.A., Minnesota Clay Co. Buffalo River State Park Malaise Trap July 3 1973 (UM). 2 females, Moorhead Clay Co..Minnn. VI–23, 27–1972 J.R. Powers Collr. (UCB). 2 females, Washington Island, Basswood Lake, Lake Co., Minn. July 14, Aug. 14, 1950 R. Namba (USNM). **Montana**: Female, Butte, Montana August 4, 1921 F.M. Sallee (USNM). **Nevada**: Female, Angel L. NEVADA 12mi. SW. Wells 11.VII.61 8400' B.H. Poole (CNC). **New Mexico**: Female, Springer N.M. CN Ainslie Collector (USNM). Male, 8 females, Santa Fe NM Cockerell collector (USNM). **Oregon**: 2 males, 5 females, Pinehurst, Ore. June 23, 1978 H.&M. Townes (HT). 4 females, Ochoco Creek VII.8, 14.28 Ore. H.&M. Townes (HT). Male, 2 females, Hyatt Reservoir VI.25, 26, 30.78 H.&M. Townes (HT). Male, Seneca, Oregon July 11 1978 H.&M. Townes (HT). Male, 8 females, Seneca, Ore. VII–11, 24–35 Joe Schuh Coll. (OSU). 2 females, Summit Prairie, Ore. VIII–3–35 Joe Schuh Coll. (OSU). Male, (Keerins Ranch) Izee, Ore. VI–25–35 Joe Schuh Coll. (OSU). Male, Ore. Deschutes Co. Tumalo St. Pk. 27 June 1961 D.R. Smith (OSU). Female, Crater Lake Park, Ore. 8mi out Medford Rd. About 5500ft. elev. Aug. 10, 1930 H.A. Scullen, Coll. (OSU). Female, Meacham, Or. 3680ft. elev. July 19, 1929 H.A. Scullen, Coll (USNM). Male, female, Indian Ford, 3200' 6mi. NW. Sisters Deschutes Co. Ore. 10.VII.65 E.&I. Munroe (CNC). Female, 7mi. SW Beatty Klamath Co. Ore. VII–10–57 J.A. Powell Collector (UCB). **South Dakota**: Female, Whitewood, S.D. July 23–1924 (USNM). Male, female, 2mi. S. Sylvan L. Black Hills, S.D. VII.11.1961 H.&A. Howden (CNC). **Utah**: 4 females, Daniels Pass, UTAH 2mi. S. Wasatch Co. 9.VII.1961 8500' B.H. Poole (CNC). 3 males, Guardsman Pass, nr. Brighton UTAH 10.VII.1961 9,800' B.H. Poole summit (CNC). 2 females, 30mi. N. of Vernal, Utah 8400' VII.8.1961 Brian Poole (CNC). 2 males, female, Duck Creek Camp Utah Kane Co. VII.11.1961 G.F. Knowlton Collector (USNM, UCD). Male, UTAH: Cache Co. Elk Valley 22 VIII 1976 G.F. Knowlton (USNM). Male, Cedar Breaks Iron Co. Utah VII–11 1961 G.F. Knowlton Collector (UCD). Female, Allens Cyn. Rich Co. Ut. VII.20–1962 G.F. Knowlton Collector (UCD). Female, Bear Canyon Mt. Nebo Ut. Juab Co. VIII.2–1962 G.F. Knowlton Collector (UCD). **Washington**: 2 males, 2 females, Mt. Rainier, Wash 2700ft, 5000' Jul. 8, VII.9 1940 H.&M. Townes (HT). 4 males, 7 females, Spokane, Wash. Sept. 74, Apr. 75 R. Oetting ex. Protagrotis obscura (USNM). Male, WASH: Oylmpic N.P. Dosewallips Rgr, Sta. VII–18–66 W. Gagne J Haddock collectors (JWC). Female, W.M. Mann Pullman Wash VII:17:08 (USNM). Female, Pullman Wash JA Hyslop Collector (USNM). Male, Uniontown Wash JM Aldrich Coll 6.26.32 (USNM). **Wyoming**: Female, Battle L. Road, Wyo. Sierra Madre Range 18.VII.1961 B.H. Poole (CNC). **Other**: Female, Wollah 6.8.88 (USNM).

INDEX TO NAMES OF TAXA

(Synonyms in italics)